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DEDICATION

VOLUME DEDICATION TO JEAN H. LANGENHEIM

- Martin Quigley*..... 1
-

NOTEWORTHY COLLECTIONS

CALIFORNIA

- GLECHOMA HEDERACEA, LINDERNIA DUBIA AND PECTIS PROSTRATA*... 3
JOHNSTONELLA ANGELICA 5
-

CONTENTS

EFFECTS OF DROUGHT AND FIRE ON NATIVE *STIPA PULCHRA* (POACEAE) RECOVERY IN SOUTHERN CALIFORNIA GRASSLANDS

- Friederike Schellenberg, Irina C. Irvine, Martha S. Witter, Anders
Taeroe Nielsen and Karsten Raulund-Rasmussen* 9
-

NEW SPECIES

TWO NEW SPECIES OF *STREPTANTHUS* (BRASSICACEAE) IN SOUTHERN CALIFORNIA, AND NOTES ON THEIR CONSERVATION

- Nick Jensen* 19
-

NEW SPECIES AND A NEW VARIETY OF *NEMACLADUS* (CAMPANULACEAE, NEMACLADOIDEAE) AND A KEY TO THE SPECIES

- Nancy R. Morin and Tina J. Ayers* 35
-

BOOK REVIEW

PLANTS OF NORTHERN CALIFORNIA, A FIELD GUIDE TO PLANTS WEST OF THE SIERRA NEVADA

- Reed Kenny* 61

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DEDICATION TO JEAN H. LANGENHEIM

Volume 67 of *Madroño* is dedicated to Dr. Jean H. Langenheim, a Professor Emerita of Biology at the University of California, Santa Cruz (Fig. 1). She is well recognized nationally and internationally as a trailblazer in several areas of the plant sciences and ecology. Her major fields of interest in biology include physiographic ecology, biochemical ecology, tropical ecology, the evolution of terpenoid-producing plants, fossil resins (amber), and the human use of plants.

Jean was born in Homer, Louisiana, in 1925, and grew up in Tulsa, Oklahoma, where she developed an interest in botany and geology. She married Ralph L. Langenheim, a geologist, in 1946 and both completed their Ph.D. degrees at the University of Minnesota. Jean studied with William Skinner Cooper, a leading plant ecologist and geobotanist, finishing her Ph.D. in 1953, a time when there were few women field scientists. Jean later published a reminiscence, “W. S. Cooper as I Knew Him: Teacher, Mentor, and Friend” [Bulletin of the Ecological Society of America 96 (2015): 184–208], in which she commented that Cooper’s efforts to give women advanced training in ecology and help them overcome hurdles had not been generally recognized. It was departmental policy at the time to allow women to do only master’s degrees, with the idea that they would become teachers. Although Cooper supported women in ecology and sponsored nine women for M.S. degrees, Jean was the only one for whom he bucked departmental policy by sponsoring her as a Ph.D. student.

Her husband Ralph took a faculty position at UC Berkeley and then at the University of Illinois at Urbana, but anti-nepotism regulations prevented Jean from obtaining a faculty position. Nevertheless she advanced her research and teaching while holding various positions, including Research Associate in the Botany Department at UC Berkeley, Assistant Professor at San Francisco College for Women, instructor in field ecology at the Rocky Mountain Biological Laboratory at Gothic, Colorado, and teacher at the University of Illinois. She pursued her research in paleobotany and ecology during these years.

In 1957 she co-authored an article with Herbert L. Mason on “Language Analysis and the Concept ‘Environment’, published in *Ecology* (38: 325–340). They applied ideas from C. W. Morris’s discussion of the theory of signs (1938) to create a definition of the word “environment” that was precise and ecologically meaningful. Ecological texts tended to adopt very broad, comprehensive definitions of the environment as the sum total of anything that might have an impact on organisms, but these conceptions were far too broad, creating the impression of overwhelming complexity.

After her divorce in 1962, Jean became a Scholar at the Radcliffe Institute for Independent Studies and a Research Fellow in the Biological Laboratories of Harvard

University. Her work took on new dimensions in the laboratory of E. S. Barghoorn, as she added chemistry to her original interests in botany and geology. At Harvard her research focused on the botanical origins of amber (fossil resin), and the ecology and evolution of tropical resin-producing trees. She worked on the genus *Hymenaea* (Fig. 2), large flowering plants mostly native to tropical America, and she formed links to Brazilian Amazonia and researchers there with help from the Harvard ethnobotanist, Richard Schultes. Jean and her students later did long-term chemical ecological research on the evolution of resin-producing trees in the equatorial tropics. She published a major reference book on this subject, *Plant Resins: Chemistry, Evolution, Ecology, and Ethnobotany*, in 2003.

In 1966 Jean returned to the University of California as Assistant Professor at the newly founded campus of UC-Santa Cruz. She was a founding member of Adlai E. Stevenson College and for many years lived in the college as a Faculty Preceptor. Her botany course, taught with Kenneth Thimann, a leading plant physiologist, was highly popular because of the way it related plants to human concerns. Their course resulted in a jointly authored textbook, *Botany: Plant Biology and Its Relation to Human Affairs*, published in 1982. She also taught graduate courses that offered new perspectives in tropical and chemical ecology, as well as the history of ecological concepts. Jean has had longstanding interests in language development and the understanding of ecological and systematic concepts, recognizing that often ecological controversies hinge on linguistic or conceptual problems. Jean was the first woman to be promoted to Full Professor at UC Santa Cruz, and her career has been an inspiration to several generations of female—and



FIG. 1. Jean at the dedication of her Faculty Vignette at the UC Santa Cruz Arboretum in 2017. Photo Credit: Martin Quigley.

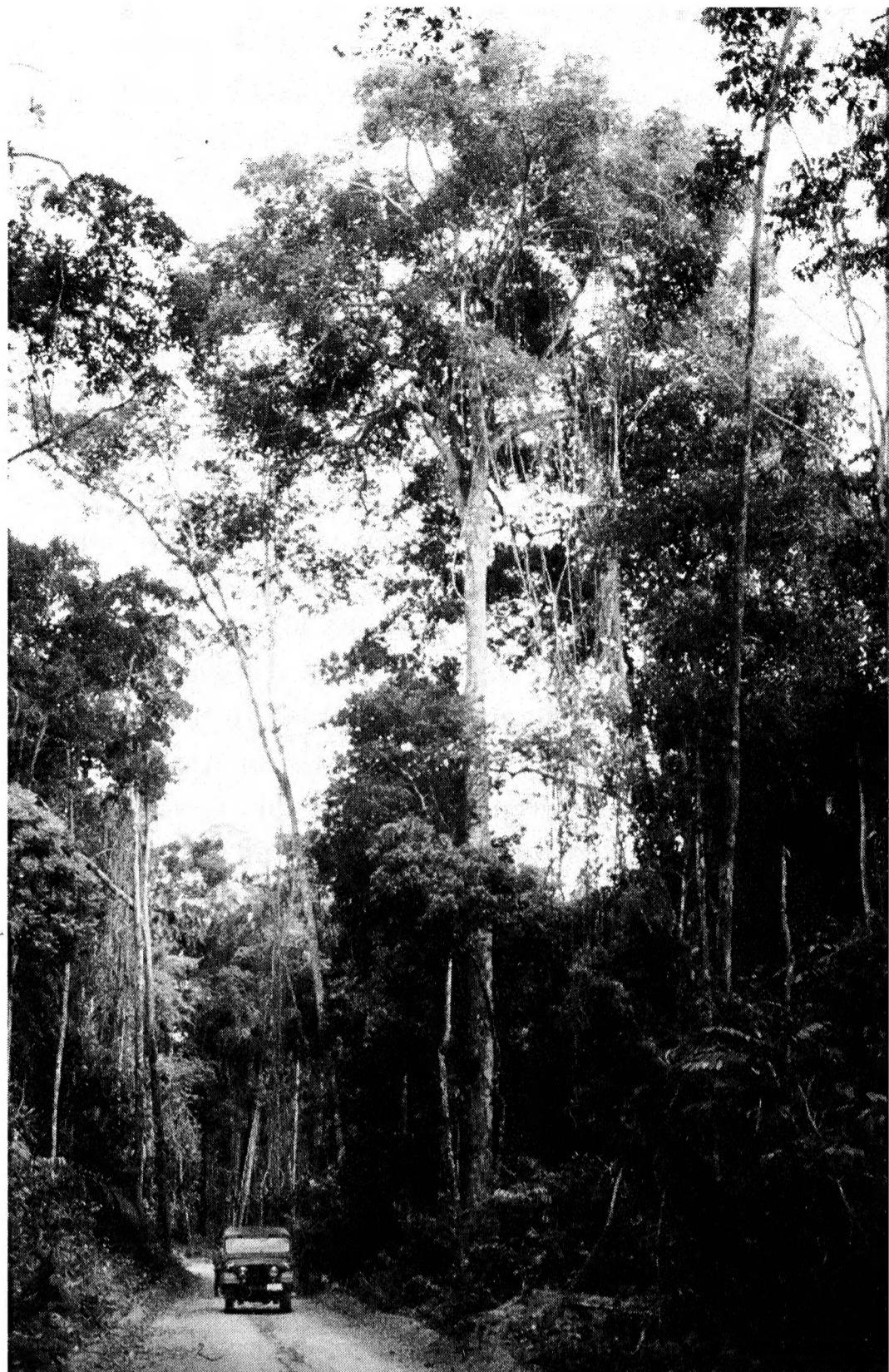


FIG. 2. Hunting *Hymenaea* in the Amazon. Photo Credit: Jean Langenheim.

male—scientists. Her contributions to UC Santa Cruz have been acknowledged with greenhouses bestowed with her name (Fig. 3) and a Faculty Vignette in the UC Santa Cruz Arboretum (Fig. 1). Her autobiography, *The Odyssey of a Woman Field Scientist: Passion, Persistence, and Patience*, was published in 2010, and is a fascinating chronicle of Jean's interests and adventures (Fig. 4).



FIG. 3. Dedication of the Jean H. Langeheim Greenhouses at UC Santa Cruz in 2018. Photo Credit: Gail Fail.



FIG. 4. Jean at a book signing for her autobiography, *The Odyssey of a Woman Field Scientist: A Story of Passion, Persistence, and Patience*. Photo Credit: Gail Fail.

The author acknowledges the Historical Records Committee of the Ecological Society of America from which this dedication is partly adapted.

—MARTIN QUIGLEY, Director, University of California Santa Cruz Arboretum and Botanic Garden, Santa Cruz, CA

NOTEWORTHY COLLECTIONS

CALIFORNIA

GLECHOMA HEDERACEA L., (LAMIACEAE).—Los Angeles Co., San Gabriel Mountains, Upper Arroyo Seco, ca. 0.6 mi. SW. of Switzer's Picnic Area, at first river crossing south of Switzer's, along E edge of trail, ± 930 m (est. Google Earth), 16 April 2015, Michael C. Long 924 and 1 May 2015, Michael C. Long 925 (RSA834592, UCR265626). *Glechoma hederacea* is a low, sprawling, herbaceous perennial found in damp soil along trail in shaded woodland of *Alnus rhombifolia* Nutt. Associated with *Artemisia douglasiana* Besser, *Boykinia rotundifolia* Parry ex A. Gray, *Erythranthe cardinalis* (Douglas ex Benth.) Spach, *Galium* cf. *angustifolium* A. Gray, *Galium aparine* L., *Phacelia* sp., *Umbellularia californica* (Hook. & Arn.) Nutt., and *Vinca major* L. Apparently naturalized as a spreading stand approx. 10m × 1.5 m in extent. Plants ca. 0.3 m high. Few flowers, lavender with darker purple spots and streaks in throat and lower petals.

Previous knowledge. Widespread in North America. Native to Europe. In California *G. hederacea* is reported from Humboldt and Shasta Cos. south to Ventura and San Bernardino Cos. (CCH1 2019).

Significance. This collection represents a first record for Los Angeles Co. and second collection for the San Gabriel Mountains. This is a range extension of about 47 km from the nearest known locality in the eastern San Gabriel Mountains, San Antonio Canyon, above Mt. Baldy Village, San Bernardino County.

LINDERNIA DUBIA (L.) Pennell (LINDERNIACEAE).—Los Angeles Co., El Monte, Peck Road Water Conservation Park (County Park). 34.100292°, -118.015114°, ca. 88m (Google Earth), 16 July, 2015, Michael C. Long 926 (RSA834596) and 24 July 2015, Michael C. Long 927 (RSA834594, UCR265621). False pimpernel occurs on the southwestern edge of broad peninsula, along South Lake, separating lakes (deep flood control basins) into two sections. It is a low growing annual that is locally common in damp, muddy soil of shoreline exposed when the lake water level is low. Plants growing in disturbed, level, drying mud flats with *Ammannia coccinea* Rottb., *Bidens frondosa* L., *Cyperus* sp., *Persicaria* prob. *lapathifolium* (L.) Delarbe, *Phalaris minor* Retz., *Salix gooddingii* C.R. Ball, *Sorghum halepense* (L.) Pers., and *Xanthium strumarium* L.

Previous knowledge. This species is widespread from Washington through southern Canada, the eastern U.S., and from Mexico to South America. In California, it is known to occur predominantly from

northern California south to Kern Co. There are also herbarium specimens from Orange and San Diego Counties. (CCH1 2019).

Significance. This is the first collection for Los Angeles Co. and one of few collections in southern California. This represents a range extension of approximately 55 km north from central Orange County (Tustin).

PECTIS PROSTRATA Cav. (ASTERACEAE).—Los Angeles Co., San Gabriel River floodplain, Irwindale, Santa Fe Dam County Regional Park, picnic area lawn near far southwestern end of lake, 34.114286, -117.957314, 142 m, 17 October 2013, Michael C. Long 921 (UCR250927, RSA820910, SD247342). *Pectis prostrata* (spreading chin-weed) was found in a waterlogged (muddy) lawn depression, a disturbed, manicured area, surrounded by turf grass, southwest of lake, and south of large covered picnic shelters. Low, prostrate, spreading annual forming individual mats up to ca. 30 cm diam. Locally very common; several hundred plants forming contiguous mats ca. 30 m × 10 m, replacing turf. Other smaller stands scattered through this area in openings in turf. Associated species: *Erigeron bonariensis* L. *Euphorbia serpyllifolia* Pers., *Malva parviflora* L., *Portulaca oleracea* L., and turf grass.

Previous knowledge. *Pectis prostrata* is native to the southern U.S. (from Arizona to Florida, including New Mexico, Texas, and Louisiana), Mexico, the West Indies, and Central America. According to SERNEC (2019), *P. prostrata* is now known from Alabama, North Carolina, Mississippi, and Nevada.

Significance. This is the first collection of this species in California (Andrew Sanders, UCR, and David Keil, OBI, personal communications). The plants were identified by Andrew Sanders and David Keil and initially appeared to be limited to a small, local population of lawn weeds in the westernmost picnic area, southwest of the recreation lake. Follow-up visits to the site over the last several years have shown the plant to have spread through the lawns, probably aided by mowing, and to have developed into enlarged stands. The plant now occurs in picnic area lawns from parking lot #6 on the west to at least parking area #4 on the east, with small stands now spreading southwestward across a paved road into wild habitat in water runoff areas (Long, personal observation). Keil, in his treatment of *P. prostrata* (Keil 2006), states “The development of roads and highways has created ideal habitats for *Pectis prostrata*. Its range

appears to be expanding along the coasts of Florida; it was discovered in Louisiana relatively recently. It can be expected to spread along the Gulf Coast and perhaps northward along the Atlantic Coast as well. Autogamy has apparently assisted *P. prostrata* to spread rapidly as suitable new habitats have become available.” The picnic area where *P. prostrata* was first found is the site of the annual Renaissance Fair in the park and this activity, bringing in horses, vehicles and equipment, is a possible source of origin of the *Pectis* population. There is certainly potential for *P. prostrata* to spread into lawns and other disturbed sites in the Los Angeles area.

It may be instructional that I made all three of these plant discoveries while birding; birders should also look down.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

JOHNSTONELLA ANGELICA (I.M.Johnston) Hasenstab & M.G.Simpson [*Cryptantha angelica* I.M.Johnston] (BORAGINACEAE). —San Diego Co., Borrego Springs, Steele/Burnand Anza-Borrego Desert Research Center, at Tilting T Drive, near south entrance, east of fence, adjacent to old dirt road going north into wash. Fine to gravelly white sand. Annual herb. Stems and leaves gray-green. Corolla white, very small, ca. 0.5 mm wide. Associated species include *Ambrosia dumosa* (A.Gray) Payne, *Cylindropuntia ganderi* (C.B.Wolf) Rebman & Pinkava, *Encelia farinosa* A.Gray ex Torr., *Ferocactus cylindraceus* (Engelm.) Orcutt, *Fouquieria splendens* Engelm., *Justicia californica* (Benth.) D.N.Gibson, *Opuntia basilaris* Engelm. & J.M.Bigelow, *Psorothamnus schottii* (Torr.) Barneby, *Stephanomeria pauciflora* (Torr.) A.Nelson, plus mixed herbs, including *Cryptantha maritima* (Greene) Greene var. *maritima*, *Diplacus bigelovii* (A.Gray) G.L.Nesom, *Eschscholzia parishii* Greene, and *Johnstonella angustifolia* (Torr.) Hasenstab & M.G.Simpson. *Jillian Stephens 1*, 12 April 2019, with *Stella Yang* and *Michael G. Simpson* (SDSU22760, SD). Upper berm of desert wash. Rare; observed only at isolated site. ca. 33.240457, -116.387903 (\pm 20 meters), 210 meters elevation. *Stella Yang s.n.* (SDSU22773), 14 April 2019. Desert wash. Rare. 33.24083, -116.38806 (\pm 20 meters), 212 meters elevation.

Previous knowledge. This species was thought to be endemic to Mexico (Rebman et al. 2016; Villaseñor 2016), with herbarium vouchers from localities in Baja California and Baja California Sur (Fig. 1). [Note that one collection, cited on SEINet (2019), from Tiburon Island, Sonora, Mexico (Felger 17753, ARIZ200386) was identified by the first author as *J. angustifolia* from the loaned specimen.] The closest known locality to the Borrego Springs population is approximately 240 miles (386 kilometers) to the south. Thus, the discovery of this disjunct population, from two nearby collections, is a new record for San Diego County, California, and the United States.

Significance. Among species of the genus *Johnstonella*—a segregate of *Cryptantha* (see Hasenstab-Lehman and Simpson 2012, Simpson et al. 2017, and Mabry and Simpson 2018)—*Johnstonella angelica* is morphologically similar in fruit morphology to *Johnstonella inaequata* (I.M.Johnston) Brand, both species having heteromorphic nutlets: one (“odd”) nutlet larger and firmly attached to the gynobase and three (“consimilar”) nutlets smaller and readily detaching. All nutlets of *J. angelica* and

J. inaequata have acute, sharp-edged (“knife-like”) margins and, as is common in the genus, whitish tubercles (Fig. 2). However, the fruit sizes of the two species are quite different. *Johnstonella angelica* has a fruiting calyx usually 2–2.1(2.5) mm long, with the large (odd) nutlet generally 0.9–1.2 mm long and the small, consimilar ones generally 0.6–0.8 long (Simpson, unpublished data; see Fig. 2A). *Johnstonella inaequata* has a fruiting calyx ca. 2.5–4 mm long, with the large (odd) nutlet ca. 1.4–1.7 mm and the small, consimilar ones ca. 1.1–1.3 mm long, (Simpson, personal observation; see Fig. 2B). In addition, *Johnstonella inaequata* has a larger corolla (2.5–4 mm limb diameter) and a stem vestiture of both antrorsely appressed and spreading trichomes. *Johnstonella angelica* has a much smaller corolla (ca. 0.5 mm limb diameter) and stems have only antrorsely appressed trichomes. *Johnstonella inaequata* is distributed considerably further north than previously known collections of *J. angelica*. Specimens of the former are recorded mostly from California (Inyo, San Bernardino, and Riverside Counties), with a few cited from Arizona (Coconino and Mohave Counties), Nevada (Clark County), and Utah (Garfield, Kane, San Juan, and Washington Counties) (CCH2 2019, SEINet 2019; see Fig. 1). (See Simpson 2007 onwards for additional images and information.)

The two Borrego Springs collections cited here are a clear match for the great majority of observed *Johnstonella angelica* specimens from Baja California and Baja California Sur, Mexico (Fig. 2C). Both of the collections resemble the typical, heteromorphic form of the species, with the large/odd nutlet having a reduced tubercle density and size, the tubercles minutely (and obscurely) spinulose. However, we note that a few examined specimens from the Baja peninsula have nutlets that are essentially homomorphic, being identical in sculpturing and gynobase attachment (all readily detaching from the fruit), with only a very slight difference in size. From herbarium specimen records cited in the CCH2 (2019) and SEINet (2019), *Johnstonella angelica* occurs in a variety of habitats, including: alluvial flats and washes, canyons/canyon bottoms, coquina-rock plateaus, dunes and upper beaches, edges of dirt or gravel roads, flats (often silty), plains/flood plains, sand and whitish sea bed substrates, slopes/rhyolitic slopes, and dry swales. This species occurs in several phytogeographic/ecoregions of the Baja peninsula, including Central Desert, Gulf Coast Desert, Magdalena Plains, Pacific Islands (Cedros Island only), and Vizcaino Desert (see Rebman et al. 2016). Curiously, it appears to be essentially absent from the Lower Colorado Desert of Baja California, the

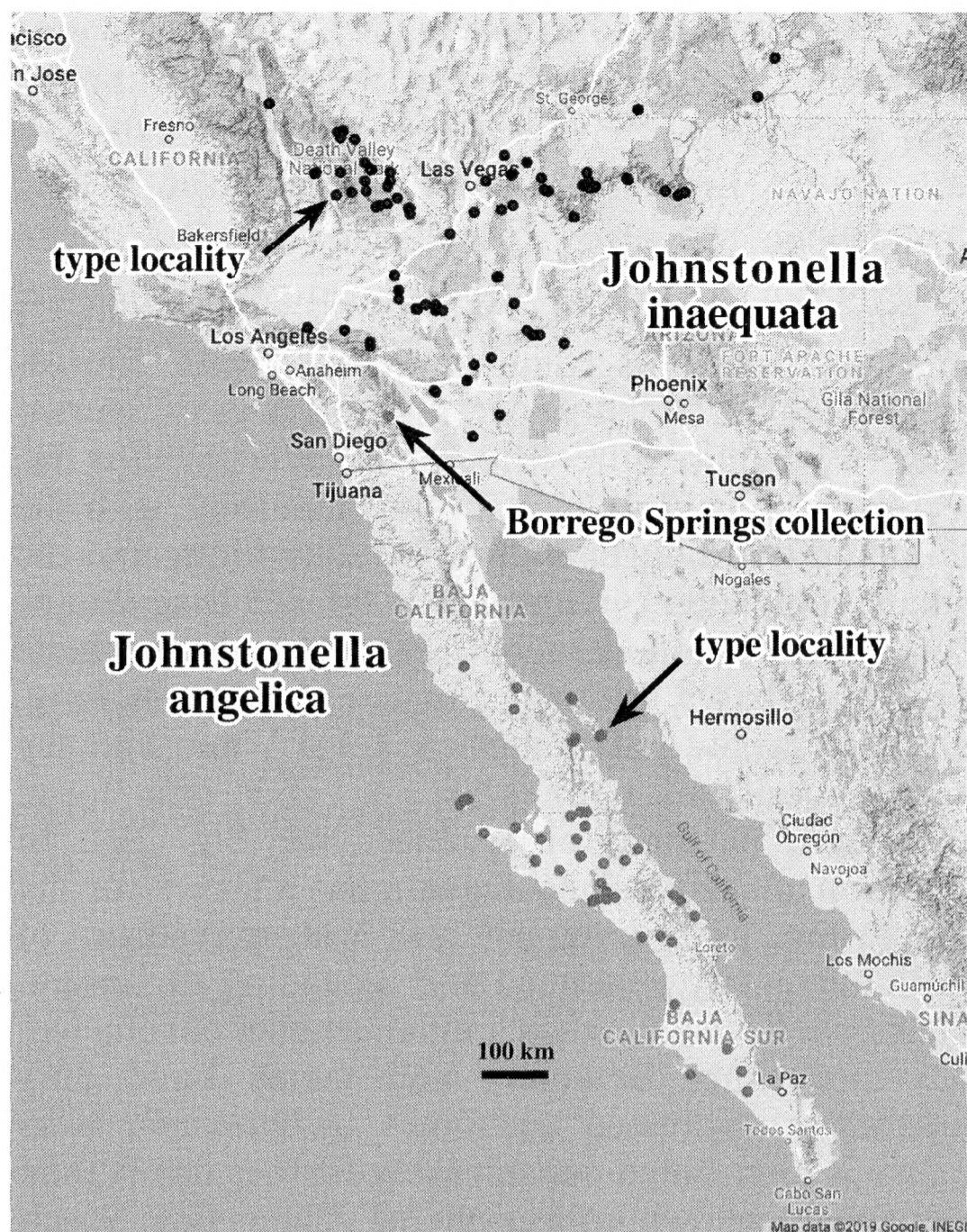


FIG. 1. Distribution map of *Johnstonella angelica* (red/gray dots) and *Johnstonella inaequata* (black dots), data from the Consortium of California Herbaria (CCH2) and SEINet Portals, both accessed 21 Sept 2019. Type localities of the two species indicated with arrows (see Johnston 1922:444, 1924:1143). Note locality of Borrego Springs collections of *J. angelica*, approximately 240 air miles (386 km) from the nearest known population of that species in Baja California, Mexico. Map data from ©Google 2019, INEGI Data.

ecoregion that includes Borrego Springs and the surrounding Anza Borrego Desert State Park.

The closest known relative of *Johnstonella angelica* from molecular phylogenetic studies (Simpson et al. 2017) is the South American *Johnstonella parviflora* (Phil.) Hasenstab & M.G.Simpson. These two species are very similar to one another in both calyx and nutlet morphology and size. In fact the two are barely distinguishable, differing slightly in large (odd) nutlet sculpturing (Simpson, personal observation, albeit from a limited number of specimens). More detailed studies will be needed to evaluate their possible conspecificity; if so, *Johnstonella parviflora* would have priority.

Johnstonella angelica could easily be confused with *J. angustifolia* (Torr.) Hasenstab & M.G.Simpson, one of the most common borages of the lower desert. In fact, the original collection by Yang s.n., 14 April 2019 cited here was a mix of the two species, indicating that they might grow adjacent to one another. However, the two can be distinguished in a number of features. *Johnstonella angustifolia* has upper stem trichomes both antrorsely appressed/

strigulose and densely short-spreading (minutely hirsute), whereas those of *Johnstonella angelica* are only antrorsely appressed/strigulose. *Johnstonella angustifolia* generally has larger corollas (varying, however, from 1–4 mm in limb diameter); the corollas of *J. angelica*, however, are quite small, about 0.5 (rarely up to 1.0) mm in limb diameter. *Johnstonella angustifolia* has a larger fruiting calyx, ca. 2.5–4 mm long; that of *J. angelica* is smaller, ca. 2–2.1(2.5) mm long. Lastly, *Johnstonella angustifolia* also has heteromorphic nutlets (very rarely homomorphic), but these generally have rounded margins and are slightly larger: the large, odd nutlets range 1.1–1.6 mm long (vs. 0.9–1.2 mm long in *J. angelica*) and the small, consimilar nutlets range 0.8–1.1 mm long (vs. 0.6–0.8 long in *J. angelica*). Interestingly, *Johnstonella angustifolia* has been observed as (rarely) having “acute” margined nutlets. This form may be due to excessive drying (personal observations, first author), but is in fact quite different from the sharp, “knife-like” nutlet margins of *J. angelica*.

Given that *Johnstonella angelica* has not knowingly been seen or collected in the Anza Borrego area before, this collection, in only two sites very near one another, may represent a waif occurrence. The species could possibly have been human dispersed, perhaps brought in on the shoes or clothing of a visiting student, scientist, worker, or tourist, or possibly on construction fill from the past, although no fill was observed in the immediate area. The dirt road adjacent to the collection site, which is barely visible and is overgrown, has only rarely been used by utility trucks in the past decade and was not involved in any construction activities when the Research Center was built between 2012 and 2014 (Jim Dice, Reserve Manager, Steele/Burnand Anza-Borrego Desert Research Center, personal communication). It is still possible that these Borrego Springs populations were animal-dispersed (likely by birds) over a long distance, not uncommon in this group (subtribe Amsinckiinae) of the Boraginaceae (see Guilliams et al. 2017). It should also be noted that this was a particularly wet season, increasing the probability of propagule germination.

Next spring, we and others will survey the region around the Steele/Burnand Anza-Borrego Desert Research Center for additional plants of this species. We urge other botanists to search for this plant in the Anza Borrego Desert State Park in San Diego County and other desert regions in the state. Herbarium vouchers are likely essential for definitive identification, but these should be collected with care so as not to extirpate local populations, if discovered. Careful examination of existing herbarium specimens, especially those identified as *Johnstonella* [*Cryptantha*] *angustifolia* or even *Johnstonella* [*Cryptantha*] *inaequata*, could reveal hidden collections of *Johnstonella angelica* from localities outside its typical range in Mexico. Although it may be difficult to determine the origin of *Johnstonella angelica* in this desert area of California in lieu of molecular

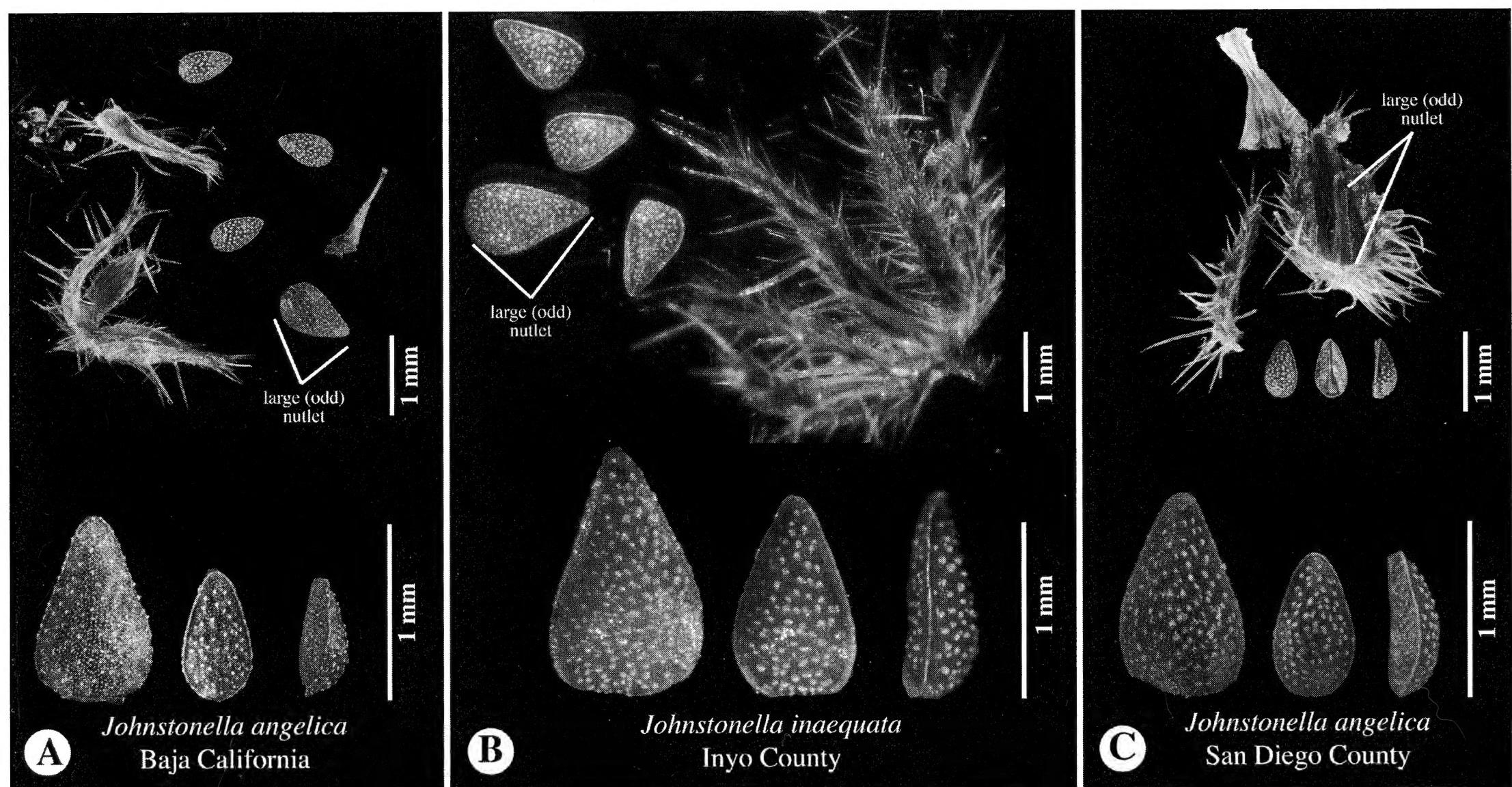


FIG. 2. Comparison of fruit morphology of *Johnstonella angelica* and *Johnstonella inaequata*. Upper images: fruits (calyces and nutlets); all to scale. Lower images: large (odd) nutlet, dorsal view at left; one of three small (consimilari) nutlet, dorsal view at middle, lateral view at right; all to scale. A. *Johnstonella angelica*, from Baja California, Mexico, upper image Wiggins 16789a, 20 February 1962 (SD00013663=SD94589), lower image Philbrick B73-262, 8 March 1973 (SBBG46949). B. *Johnstonella inaequata*, from Death Valley, Inyo County, California; all images: André 8132, 31 March 2006 (RSA0116520=RSA732141). C. *Johnstonella angelica*, from Borrego Springs, San Diego County, California, Stephens 1, 12 April 2019 (SDSU22760).

studies, the discovery of additional populations in the area might provide support for hypotheses that the species is indigenous or has become permanently established in California. Additional information will be needed before the species can be evaluated for possible California Rare Plant ranking (California Native Plant Society Rare Plant Program 2019).

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EFFECTS OF DROUGHT AND FIRE ON NATIVE *STIPA PULCHRA* (POACEAE) RECOVERY IN SOUTHERN CALIFORNIA GRASSLANDS

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ABSTRACT

Mediterranean-type climate California experiences both frequent wildfires and periodic drought. Climate change models predict increased severity of drought, and wildfire size and frequency, leading to concern about the ability of some plant species to recover to pre-fire conditions when wildfires and drought coincide. During exceptional drought, drought-adapted native vegetation, such as perennial native grassland, can experience substantial die-off. Here we use three post-fire case studies in southern California to assess the combined effects of fire and drought on the resilience of a native perennial bunchgrass, *Stipa pulchra* Hitchc. (Poaceae). We hypothesized that resilience to fire, assessed as post-fire survival, resprouting and fecundity (i.e., number of flowering plants and inflorescences), would decrease if the fire occurred during a drought. Unburned (control) sites had about double the survival and resprouting, and about three times the fecundity compared to moderate-severity burn sites. Resprouting and fecundity in the low-severity burn sites was about twice that of moderate-severity burn sites, and survival was five times higher. Responses to two springtime fires that occurred during drought were similar (average mortality 37%), in contrast to a fall fire with no drought (6%). We cannot separate the relative contribution of drought effects from those of the time of year (spring vs. fall), burn severity, and other site factors. However, moderate-severity burns, in combination with drought, decreased survival, resprouting, and fecundity of *S. pulchra*.

Key Words: California grassland, climate change, drought, fire, purple needlegrass, *Stipa pulchra*.

Fires and periodic droughts are integral parts of the Mediterranean-type climate and ecosystem of southern California. With current changes in climate, those events are experiencing dramatic changes in extent and frequency. Much of the western United States, especially southern and mountain ecoregions, has seen an increase in large fire incidents, especially since the beginning of the twenty-first century (Dennison 2014; Keeley and Syphard 2019). In addition to increasing wildfires, large parts of southern California experience prolonged drought cycles. For the California south coast, ten years have had below average rainfall-years since 2000, with record lows occurring in 2001-2002 (162 mm), and 2006-2007 (138 mm) (NOAA 2019). Exceptionally high temperatures along with the timing and amount of rainfall from 2012 through 2016, created record drought conditions (213 mm in 2012-13, 194 mm in 2013-14, 375 mm long-term average) (Griffin and Anchukaitis 2014; NOAA 2019; WRCC 2015a, b).

Drought and high temperatures have affected nearly every native vegetation type in California (Vose et al. 2016) making them more vulnerable to

direct or secondary causes of mortality, such as pathogen and pest infestations. Of particular concern are the impacts to native California perennial grasslands, an important vegetation type that is in serious decline (Stromberg et al. 2007).

Patches of native California grasslands have persisted throughout the state despite the increasing dominance of invasive, non-native annual grasses (Hamilton 2002). *Stipa pulchra* Hitchc. (Poaceae), a drought and fire-adapted native bunchgrass, is one of the main constituents of California's native grasslands. Native grasslands play important ecological roles and provide ecosystem services such as food sources for wildlife, erosion control (Tilley et al. 2009), and carbon storage (Koteen et al. 2011).

Concern about the loss of native grasslands has initiated studies on the competition of native bunchgrasses with non-native annual grasses and forbs (Dyer and Rice 1997; Hamilton et al. 1999), as well as the effects of grazing and fire (D'Antonio et al. 2002; Bartolome et al. 2004; Marty et al. 2005). Studies of fire effects on *S. pulchra* have shown an inconsistent response (Reiner 2007). While some

have suggested at least short-term positive responses of burning (Dyer et al. 1996; Moyes et al. 2005), others have found no effect or that *S. pulchra* responded negatively to fire (Dyer and Rice 1997; Bartolome et al. 2004). Little is known about the effects of fire severity and fire season on *S. pulchra*, but these factors, along with other site-specific characteristics, are important predictors of post-fire recovery in California grasslands (Klinger and Messer 2000). Despite this knowledge gap, some studies have suggested that variations in rainfall pattern and drought may override burning and grazing effects by increasing mortality (Marty et al. 2005), and reducing fecundity and survival of *S. pulchra* (Hamilton et al. 1999; Bartolome et al. 2004). Previous-year rainfall patterns have been recognized as especially important for grasslands dominated by perennial species, like *S. pulchra* (Dudney et al. 2016).

Climate change models for southern California predict increasing temperatures while predictions for future trends in precipitation are highly variable on a fine scale (Field et al. 1999; Cayan et al. 2008). Regardless of future changes in precipitation, higher temperatures will lead to an increase in evapotranspiration and drought (Sandel and Dangremond 2012; Griffin and Anchukaitis 2014). There is agreement that those climatic changes will favor traits in annual non-native grasses that are competitively superior to native grassland species (Lenihan et al. 2008; Sandel and Dangremond 2012). An increase in non-native annual grass biomass would contribute to more fine flammable fuel, promoting favorable conditions for more frequent fires that could reduce the cover of perennial species (Keeley and Syphard 2019).

Understanding the synergistic effects of fire and drought on *S. pulchra* grasslands is necessary for conservation and restoration efforts, especially with regards to climate change. We conducted an observational and comparative study examining the effects of fire and different climatic conditions on *S. pulchra* mortality, resprouting and fecundity surrounding three fires in southern California. First, we focused on *S. pulchra* vigor in burned and unburned plots after a fire that occurred during drought, taking into account that it burned at two different severities, low and moderate. Since the burned and unburned sites are spatially separated, we have no control over site-specific characteristics, which introduced limitations to this study. Secondly, we compare those findings to existing post-fire *S. pulchra* recovery data from two fires that burned during drought and in wet conditions, respectively. We acknowledge that the differences in severity, year, season and site can have confounding effects on our results. We hypothesized that *S. pulchra* mortality following fire during drought would increase, and resprouting and fecundity would decrease when compared to non-drought fire recovery.

METHODS

Study Species

Stipa pulchra is found primarily on valley bottoms and stony foothills on deep soils with high clay content (Sawyer and Keeler-Wolf 1995). Reproduction occurs by wind pollination and by tillering and fragmentation of bunches (Steinberg 2002). The latter allows the plant to recover from defoliation of intensive grazing and fire (Steinberg 2002). It senesces in the summer after seed production and resprouts in the rainy season (Tilley et al. 2009). *Stipa pulchra* is fire tolerant and responds to fire by growing new tillers from meristems (Steinberg 2002).

Study Sites

The study was conducted at six sites in the Santa Monica Mountains National Recreation Area (SMMNRA, U.S. National Park Service), located in Ventura and Los Angeles Counties of southern California, USA. The SMMNRA is an approximately 62,000-ha park located in the Mediterranean-type climate region of California with summer drought and winter rainfall. Average annual precipitation in Los Angeles County in the period from 1877 to 2015 was 375 mm, and 373 mm in Ventura County, though there is high year-to-year variation (WRCC 2015a, b).

The fire that prompted the study was the 2013 Springs Fire. The Springs Fire started May 2, 2013 and burned 9,814 ha on the west end of the SMMNRA. Our site selection criteria included: 1) the presence of native perennial grasslands dominated by *S. pulchra*, and 2) known drought and fire history of the site. Three of the sites, Rancho Sierra Vista, Deer Creek Canyon, and La Jolla Valley, were located in areas that burned in the Springs Fire (Figs. 1A, 1B, 1C). We classified burn severity of the sites according to the 5-point Fire Monitoring Handbook burn severity scale (USDI National Park Service 2003). Low-severity burn (LS) sites were those where *S. pulchra* tussocks were only mildly scorched or partially burned. Moderate-severity burn (MS) sites were those where tussocks were completely burned and had less residual biomass. Burn severity was moderate in Deer Creek Canyon and La Jolla Valley and low at Rancho Sierra Vista. This site was burned in a low intensity, nighttime prescribed backfire that was set to protect nearby historic structures, in contrast to Deer Creek and La Jolla Valley, where moderate fire intensity occurred under daytime, wind-driven wildfire conditions. Pre-fire fuel loads were considered comparable at all three sites. Three unburned control (UB) sites were selected for data collection in 2014. Adequate time had passed since their last fires prior to this study to consider them recovered (Table 1). Paramount Ranch burned in the 1982 Dayton Fire (Fig. 1D), Palo Comado Canyon and Cheeseboro Canyon burned in the 2005 Topanga

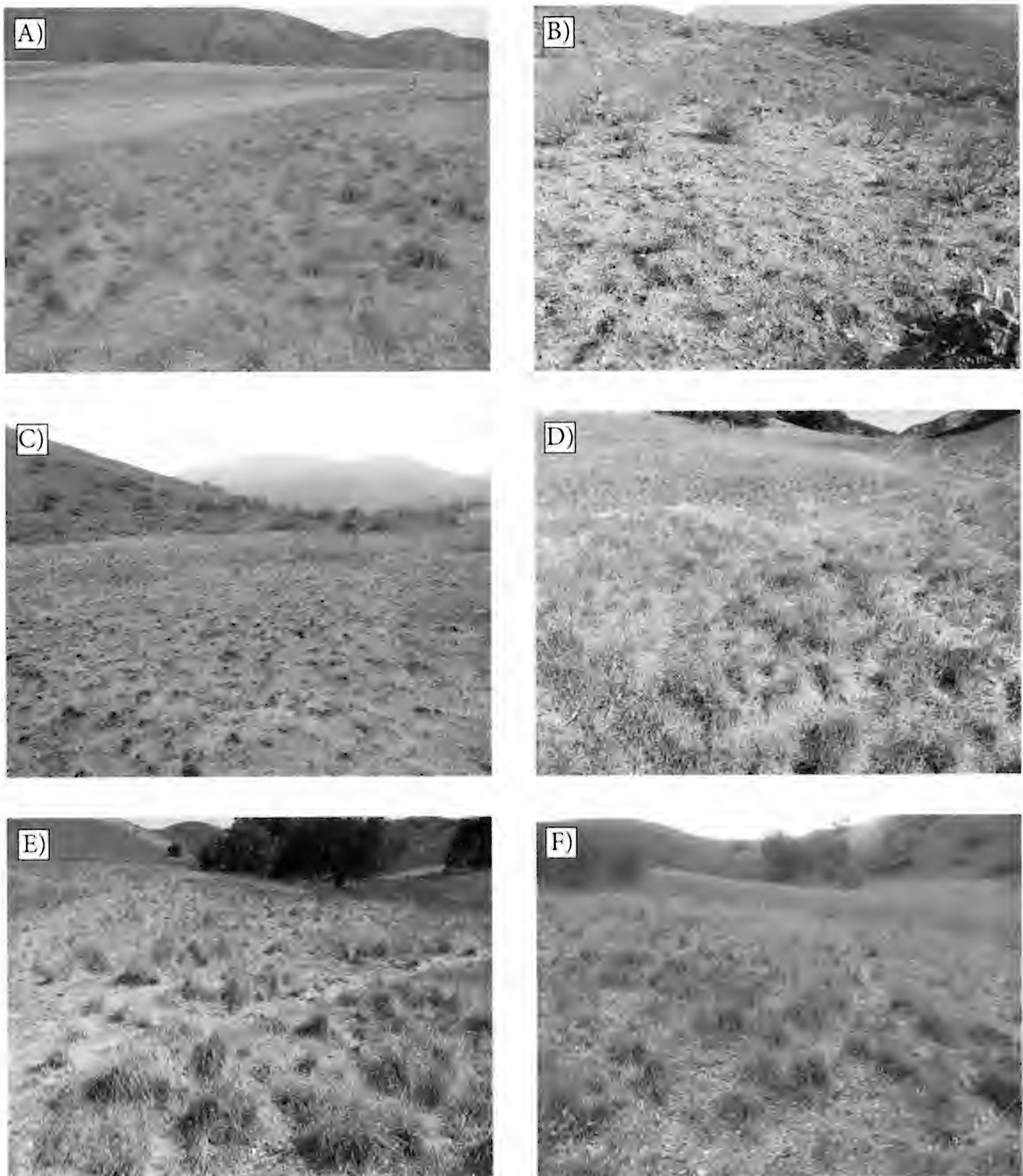


FIG. 1. Photo example of the conditions at the six study sites. A) Rancho Sierra Vista, B) Deer Creek Canyon, C) La Jolla Valley, D) Paramount Ranch, E) Palo Comado Canyon, and F) Cheeseboro Canyon.

Fire (Figs. 1E, 1F). The Springs Fire occurred in a period of record low rainfall and record high temperature (Griffin and Anchukaitis 2014). For the water-years 2013 and 2014, annual precipitation averaged 213 mm and 196 mm, respectively. Temperatures averaged 16.4 °C and 17.3 °C. The 20th century average precipitation for the California south coast was 457 mm and temperature was 14.9 °C (NOAA 2019).

For comparison we used the post-fire monitoring data from two other fires. The Topanga Fire started on September 28, 2005 and burned 9,783 ha in the northern, central portion of the SMMNRA (Table 1). Data were collected in Cheeseboro and Palo Comado Canyons. Average annual precipitation for the 2005 and 2006 water-years was 878 mm and 412 mm, respectively. Average temperatures were 15.5 °C and 16.2 °C, respectively. On April 16 and 17, 2002 a

TABLE 1. FIRE AND CLIMATE INFORMATION AT STUDY SITES. Climate data was derived from NOAA (2019). Water-year precipitation includes precipitation from October to September. Water-year precipitation during fire includes the year when the fire occurred. Post-fire water-year precipitation shows conditions for the following water-year. See USDI National Park Service (2003) and main text for more information about how burn severity was classified. The asterisk (*) indicates a site that, prior to the Woolsey Fire, last burned in the 1982 Dayton Fire.

Year	Fire	Sites	No. plots	Fire season	Water-year precip. during fire (mm)	Water-year precip. post-fire (mm)	Water-year temp. during fire (°C)	Water-year temp. post-fire (°C)	Burn severity
2002	Cheeseboro Fire	CH	14	Spring	164	477	15.8	16.2	moderate
2005	Topanga Fire	CH	19	Fall	878	412	15.5	16.2	moderate
		PC	42						moderate
2013	Springs Fire	DC	6	Spring	213	196	16.4	17.3	moderate
		LJV	72						moderate
		RSV	7						low
	NA	CH	11	NA					NA
		PC	13						NA
		PR*	7						NA

prescribed burn was set in Cheeseboro Canyon (i.e., the Cheeseboro Fire) during a period of drought (NOAA 2016). For the 2002 and 2003 water-years, annual average precipitation was 164 mm and 477 mm, respectively (Table 1). The average annual temperature was 15.8 °C for 2002 and 16.2 °C for 2003.

Data Collection

Mapping perennial grass patches and plot selection. Between May 28 and June 6 2003, approximately one year after the Cheeseboro Fire, one transect (13 m long, with 13 1×1 m subplots) was located in the burned area and data on *S. pulchra* mortality, tussock diameters, and flowering status (see below for details on how these parameters were measured) were collected. Following the Topanga Fire, the geographic location and spatial extension of the Cheeseboro Canyon and Palo Comado Canyon *S. pulchra* patches were mapped. Data on mortality, tussock diameters, resprouting, resprout pattern, and flowering status were collected from August 3 to October 3, 2006. At this time, permanent 1×1 m plots were established in the mapped patches. All Springs Fire data were collected in October and November 2014 before the onset of the winter rain season, 17 to 18 months after the fire. We used the Topanga Fire maps to relocate the patches. At each of our six study sites, we mapped the *S. pulchra* patches with a GPS unit with sub-meter accuracy (Trimble Geo XT™, Trimble Inc., Sunnyvale, CA). We collected data from the permanent plots located near the center of the patch. We randomly placed one 1×1 m plot in the center of patches without existing plots or where the pre-existing plots were not in the center of the patch. The analysis of the Topanga Fire data (Witter and Sikes 2006) showed that the centers of the patches were denser and more intact, but had no differences in mortality, compared to the edges.

Thus, to determine burn severity effects between the LS, MS, and UB patches, we considered the patch interiors to be more characteristic and less variable than edges. Because of the large size variation of the patches, we adjusted the number of plots according to patch size and shape, ranging from one to eight plots per patch. The plots were equally distributed in each patch and within the grassland to represent potential variation in grassland composition and environmental variables. To ensure randomization of the plot location, we separated larger patches into approximately equally sized parts and randomly placed plots in the center of each of these parts. We established a total of 116 plots (72 in La Jolla Valley, 7 in Rancho Sierra Vista, 6 in Deer Creek, 13 in Palo Comado Canyon, 11 in Cheeseboro Canyon, and 7 in Paramount Ranch). La Jolla Valley received the bulk of these plots, causing our dataset to be unbalanced (addressed in Data Analysis section below). This is because the Springs Fire provided the opportunity to complete a larger mapping project of the extensive native grassland at the La Jolla Valley Natural Preserve, established in 1972 by the California Department of Parks and Recreation to protect native grasslands.

We recorded the patch characteristics slope, aspect, elevation and patch size (ha). To determine the percentage of mortality, all individual *S. pulchra* plants were counted as either live or dead. Because *S. pulchra* tussocks are typically elliptical in shape, we measured their base on two perpendicular diameters to calculate the average total tussock area per individual. We visually estimated the percent of the tussock area that resprouted of each living plant, where a fully recovered plant with leaves in the center and on the edge would be classified as having 100% recovery. The percentage of the plant that resprouted in the unburned plots (UB), refers to the visible rate of recovery from dormancy. To determine resprouting pattern, we differentiated between resprouting on the tussocks' edge and other parts to estimate how much of the interior of the plant had died. We

TABLE 2. DEPENDENT AND INDEPENDENT VARIABLES TESTED. In 2003, we were only able to test mortality and flowering. In 2006, we were only able to test mortality, resprouting, resprout pattern and flowering.

Dependent variable	Description
Mortality (%)	Percent of <i>S. pulchra</i> individuals that died
Resprouting (%)	Percent of tussock area of <i>S. pulchra</i> that resprouted
Resprouting on edge (%)	Percent of <i>S. pulchra</i> individuals that resprouted on the edge of the tussock
Flowering (%)	Percent of <i>S. pulchra</i> individuals that produced flowers
Number of inflorescences (count)	Average number of inflorescences among <i>S. pulchra</i> individuals that flowered
NPG cover (%)	Percent cover of native perennial grass on a patch level
NNAG cover (%)	Percent cover of non-native annual grass on a patch level
Independent variable	
<i>Burn severity</i>	
Unburned	Unburned sites (Cheeseboro Canyon, Palo Comado Canyon, and Paramount Ranch)
Low-severity burn	Low-severity burn site (Rancho Sierra Vista)
Moderate-severity burn	Moderate-severity burn sites (Deer Creek Canyon, La Jolla Valley)
<i>Year</i>	
2003	
2006	
2014	Low-severity burn
2014	Moderate-severity burn

recorded whether the plant was flowering and counted the number of inflorescences to describe reproductive output.

Plant community composition. While the patches were *S. pulchra*-dominated, other species were present at low abundance. We visually estimated the percent cover of all species in each patch. For the Cheeseboro and Topanga Fires, no data on plant community composition were collected. Species that were present at trace levels were assigned a cover value of 0.2%. We classified all species into functional groups and used an average of $\geq 5\%$ cover as a cut-off for inclusion in the analysis, yielding native perennial grass (NPG) and non-native annual grass (NNAG) as the two functional groups consistent among all patches. NPG was represented by only one species, *S. pulchra*. NNAG included slender oat (*Avena barbata* Pott ex Link), ripgut brome (*Bromus diandrus* Roth), red brome (*Bromus madritensis* L.), and perennial ryegrass (*Festuca perennis* L.).

Data Analysis

Spring Fire burned and unburned sites. We used individual linear models to test for significant relationships between the response variables mortality, resprouting, resprout pattern, flowering, number of inflorescences, NPG and NNAG, and the independent variables associated with patch-specific characteristics slope, aspect, elevation and patch size. For aspect we used a cosine transformation to convert degrees to a continuous scale (Beers et al. 1966), and used a linear model to test for relationships between response variables and transformed aspect. If we found any significant relationships between the response variables and the patch-specific characteristics, we proceeded to use a linear

mixed model framework to test for the effect of burn severity on response variables, and included patch as a random effect to account for differences in patch characteristics. The linear mixed models included the fixed effect, burn severity (treatment: unburned, low-severity burn, moderate-severity burn). The response variables were mortality, resprouting, resprout pattern, flowering and number of inflorescences (Table 2). To analyze the effect of burn treatment on number of inflorescences, we averaged the number of inflorescences by dividing the total number of inflorescences per plot by the number of flowering *S. pulchra* individuals. Burn severity effects on percent cover of NPG and NNAG were analyzed using the same linear mixed-model described above.

We conducted all analysis in R version 3.5.0 (R Core Team, R Foundation for Statistical Computing, Vienna, Austria) using the function *lmer* in the package *lmerTest* (Kuznetsova et al. 2017). We visually checked model residuals for goodness of fit. We then calculated least squares means for each treatment level using the *lsmeans* function in the package *lsmeans* (Lenth 2016). For each independent variable, we used the *lsmeans* function to calculate pairwise comparisons of means between burn severity levels using Tukey's HSD, with $\alpha = 0.05$ as a cutoff for determining significance.

Comparisons between fires. To test for the synergistic effects of drought and fire on *S. pulchra* mortality and fecundity, we used the same mixed-model described above with mortality, resprouting, resprout pattern and flowering as the dependent variables and year as the independent variable, with patch nested within site as the random effect. We used year as our independent variable because it coincided with a specific climate and fire combina-

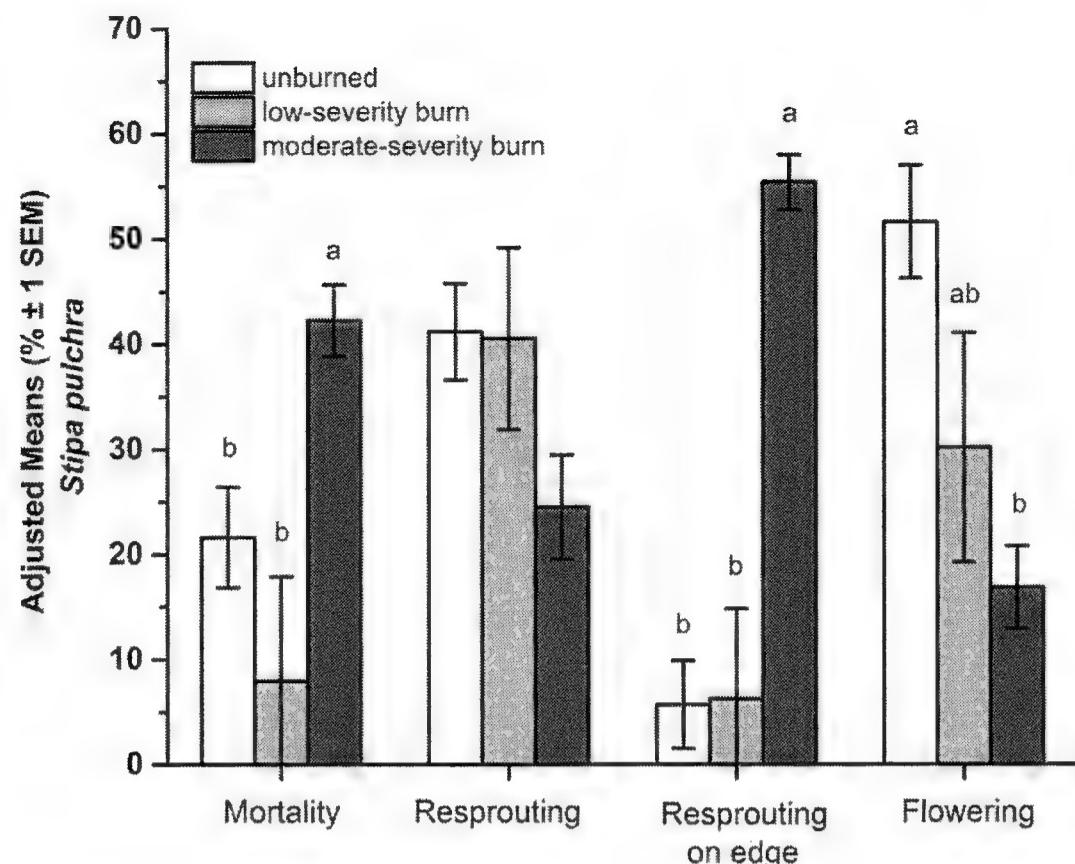


FIG. 2. Fire effects of burned and unburned sites in the Springs Fire assessed as mortality, resprouting, resprouting on edge, and flowering. Bars represent LS means \pm SE. Means with different letters are significantly different (Tukey's HSD, $P < 0.05$).

tion. Data from the Springs Fire burned sites were sorted into low-severity and moderate-severity.

RESULTS

Springs Fire Burned and Unburned Sites

We found significant ($P < 0.05$) relationships between patch characteristics (slope, transformed aspect, elevation, patch size) and dependent variables (Appendix 1). We were therefore justified in including patch as a random effect in our mixed models to account for differences in patch characteristics.

Mortality. Mortality was about twice as high in the MS plots compared to the UB plots (MS: $42\% \pm 3$ SE, LS: $8\% \pm 10$ SE, UB: $22\% \pm 5$ SE; Fig. 2).

Resprouting. Resprouting in LS and UB plots was similar. However, the mean resprouting rate was around 60% of that at MS sites than at UB and LS sites (MS: $25\% \pm 5$ SE, LS: $41\% \pm 9$ SE, UB: $41\% \pm 5$ SE). The resprout pattern was different in MS compared to LS and UB sites. Only about $6\% \pm 4$ SE of the UB and LS grasses resprouted on the tussock edges, whereas $55\% \pm 3$ SE of the MS plants showed this pattern.

Flowering. In UB sites, $52\% \pm 5$ SE of *S. pulchra* individuals flowered, whereas only $30\% \pm 11$ SE of the LS and $17\% \pm 4$ SE of the MS grasses flowered. There was no significant difference in the average number of inflorescences per individual between UB and LS, UB and MS and between LS and MS (UB: 4.6 ± 1.2 SE, LS: 2.6 ± 2.4 SE, MS: 3 ± 1.5 SE).

Plant community composition. Cover of NPG was highest in the UB patches, followed by the LS site and MS patches (UB: $33\% \pm 3$ SE, LS: $25\% \pm 5$ SE,

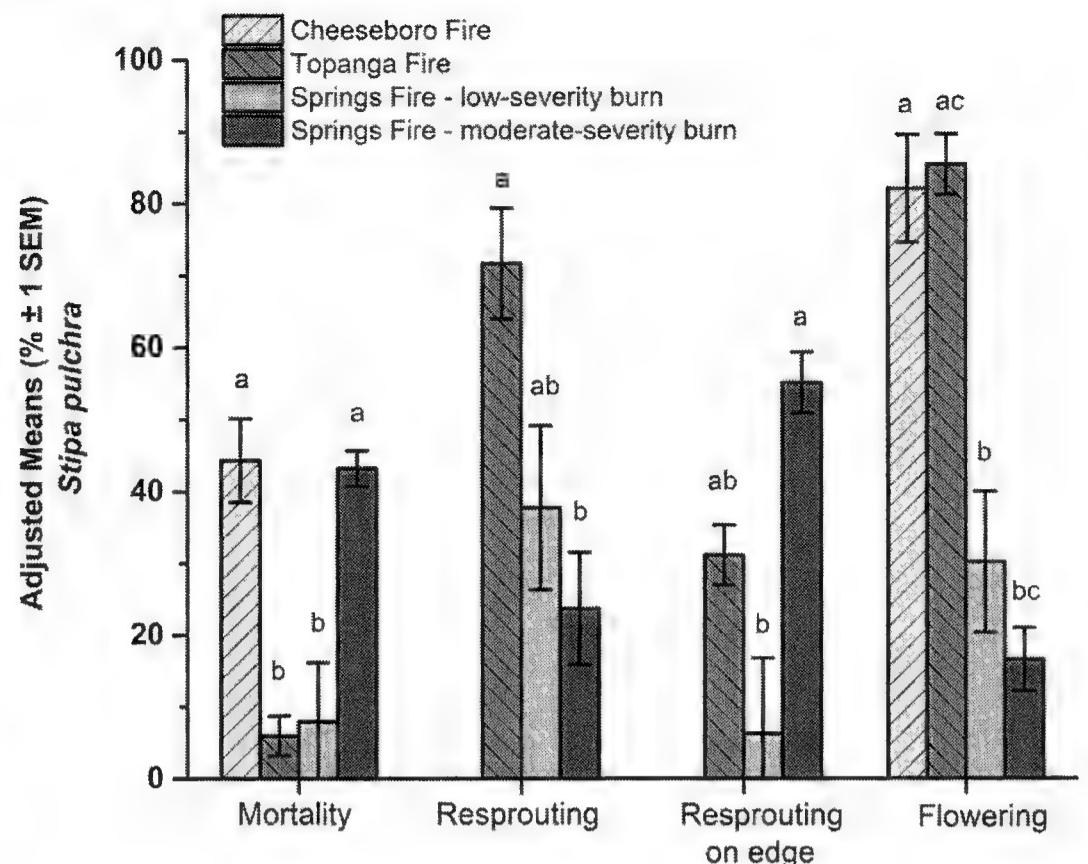


FIG. 3. Fire effects of burned sites of Cheesboro Fire, Topanga Fire and Springs Fire assessed as mortality, resprouting, resprouting on edge, and flowering. Bars represent LS means \pm SE. Means with different letters are significantly different (Tukey's HSD, $P < 0.05$).

MS: $9\% \pm 2$ SE). Pairwise comparison revealed significant differences between the UB and MS patches ($P < 0.001$) and between LS and MS patches ($P = 0.007$). The average cover of NNAG was highest in the LS patches and lowest in the MS patches (UB: $8\% \pm 2$ SE, LS: $13\% \pm 4$ SE, MS: $5\% \pm 1$ SE), and similar in MS and UB patches. However, the cover was about three times higher in the LS patches compared to the MS patches ($P = 0.04$).

The LS patches at Rancho Sierra Vista were similar to UB patches ($P = 0.19$) and different from MS patches ($P = 0.007$). NPG cover at Rancho Sierra Vista was most similar to that of Paramount Ranch, which burned in 1982. The average percent cover of NNAG at the LS patches was also similar to the UB patches ($P = 0.23$) and different from MS patches ($P = 0.04$).

Comparisons between Fires

The Topanga Fire and the Springs Fire. The Springs Fire data show that mortality in MS plots in Deer Creek and La Jolla Valley was seven times higher than the mortality after the Topanga Fire (Fig. 3; Topanga Fire: $6\% \pm 3$ SE, Springs Fire MS: $43\% \pm 2$ SE). Mortality in the LS Rancho Sierra Vista plots did not differ significantly from that measured after the Topanga Fire (Springs Fire LS: $8\% \pm 8$ SE). The fraction of the tussock area that resprouted in the Springs Fire MS plots was a third of the resprouted area after the Topanga Fire (Topanga Fire: $72\% \pm 8$ SE, Springs Fire MS: $24\% \pm 8$ SE). The tussock area that resprouted in the Springs Fire LS plots was about half that of the Topanga Fire plots (Springs Fire LS: $38\% \pm 11$ SE). Resprouting on the edges of burned plants did not differ between the Topanga and the Springs Fire

(Topanga Fire: $31\% \pm 4$ SE, Springs Fire LS: $6\% \pm 11$ SE, Springs Fire MS: $55\% \pm 4$ SE).

S. pulchra fecundity was more reduced after the Springs Fire with drought than after the Topanga Fire with wet conditions. The number of flowering plants after the Topanga Fire was almost three times higher than in the LS plots and five times higher than in the MS plots of the Springs Fire (Topanga Fire: $85\% \pm 4$ SE, 2014 LS: $30\% \pm 10$ SE, Springs Fire MS: $17\% \pm 4$ SE).

The Cheeseboro Fire and the Springs Fire. Like the Springs Fire, the Cheeseboro Fire occurred in the springtime during a drought, though not as severe drought as in 2013. *S. pulchra* mortality was similar between the Cheeseboro Fire and the Springs Fire MS plots (Cheeseboro Fire: $44\% \pm 6$ SE, Springs Fire LS: $8\% \pm 8$ SE, Springs Fire MS: $43\% \pm 2$ SE). The number of burned *S. pulchra* that produced flowers was almost five times higher after the Cheeseboro Fire than found in the MS plots, and 2.7 times higher than in the LS plots of the Springs Fire (Cheeseboro Fire: $82\% \pm 7$ SE, Springs Fire LS: $30\% \pm 10$ SE, Springs Fire MS: $17\% \pm 4$ SE).

DISCUSSION

Effects of Drought and Fire on *S. pulchra* after the Springs Fire

While many studies have tested fire effects on native perennial grasses, mainly focused on *S. pulchra*, this species does not seem to respond to fire in a consistent way (Reiner 2007). Differences in timing of burning and fuel loads alone do not seem to justify the varying responses. While we found decreased survival, regrowth and fecundity after moderate-severity fire, there are factors that may have impacted our results. Due to the study design and the area that burned in the Springs Fire, there was no ability to control for biotic, abiotic or other site differences that may have affected the plant communities. One parameter that varied across sites was the soil (USDA Natural Resources Conservation Service 2006). Other differences between sites were the micro- and mesoclimate, especially in consideration of the proximity to the ocean. The burned sites, La Jolla Valley, Deer Creek Canyon, and Rancho Sierra Vista, are closer to the Pacific Ocean and receive more coastal fog than the unburned sites located more inland. Corbin et al. (2005) have shown that native perennial bunchgrass species benefit from summer coastal fog. We cannot exclude the possibility that these factors may have affected the responses we measured. However, climate and especially the rainfall pattern have been recognized as strong factors in predicting *S. pulchra* mortality and potentially play more important roles than both fire and site characteristics (Dyer et al. 1996;

Hamilton et al. 1999; D'Antonio et al. 2002; Bartolome et al. 2004; Marty et al. 2005).

In their review, D'Antonio et al. (2002) summarized that climate, and precipitation especially, is more important than type of burning to influence the response of native perennial grasses to fire, though our results indicate that low severity burns are less detrimental to *S. pulchra*. Burn severity was most likely a factor influencing mortality, resprouting, and fecundity, with moderate-severity fire having a greater negative effect than low severity fire. Due to a lack of replicates of burn severity independent of site, we cannot exclude site-related factors also having influenced recovery. Interpreting burn severity as being important for recovery is consistent with observations that greater biomass loss (i.e., higher burn severity) had a slower recovery to pre-fire conditions (Langstroth 1991).

We expected to find low cover of non-native species in the burned sites. Potts et al. (2012) found that fewer non-native species emerged in burned areas in low precipitation years. However, we found no difference between LS or MS and UB sites. In an experiment testing the interactions between NNAG and *S. pulchra* during different life stages, Hamilton et al. (1999) found stronger negative effects of drought, especially early in the growing season, on NNAG seedlings than on *S. pulchra* seedlings. Prolonged drought, like the exceptional drought from 2012-2016, the most severe drought in the last 1200 years (Griffin and Anchukaitis 2014), might have had a greater effect on NNAG due to their short-lived seed bank (~ 1 year), reducing their cover in the UB sites to levels comparable to burned sites. For the MS sites, this result also indicates that non-native species did not become dominant competitors during drought where fire reduced the survival of *S. pulchra*. This is in contrast to findings in average rainfall years where non-native cover increased after fire (Witter and Sykes 2006). Since the cover of NPG and NNAG at the LS site was similar to the UB sites, we conclude that the low-severity fire did not adversely affect the species assemblage, in contrast to the MS sites where the cover of NPG declined.

Effects of Different Fires and Climatic Conditions

Comparing the effects of different fires and climatic conditions from multiple years on the recovery of *S. pulchra* has limited our ability to draw clear conclusions. We acknowledge that the differences in sites, fire characteristics, season of burn and data collection between years, as well as the long time between observations, may have impacted our results. Nevertheless, we found support for our hypothesis that post-fire mortality would be significantly higher, and that resprouting and fecundity would be reduced with drought, as opposed to during wet conditions. Although we are unable to distinguish the contribution from the

season of burning (spring vs. fall). Marty et al. (2005) associated a growth boom of *S. pulchra* with differences in climatic patterns, concluding that events associated with El Niño Southern Oscillation, such as higher rainfall, can have positive effects on *S. pulchra* growth. In the water-year 2005, before the Topanga Fire started towards the end of that water-year, there was a significant rainfall event associated with El Niño patterns and it is likely that this event positively contributed to the performance of *S. pulchra* that we observed. Similarly, Hamilton et al. (1999) suggest that high rainfall years are particularly favorable for *S. pulchra* seedling recruitment. However, an experimental design taking into account other site factors, such as soil, and season of fire would be needed to further support our findings.

Interestingly, we found elevated mortality, and reduced flowering and resprouting in the unburned plots in the Springs Fire compared to the Topanga Fire's burned plots. Because of the nonconformity in treatment type and year we did not include these findings in the results. Nevertheless, they indicate a trend that drought might have more severe effects on *S. pulchra* than fire in a year with sufficient rainfall. Bartolome et al. (2004) found that rainfall pattern can significantly alter *S. pulchra* and the native perennial grass, California oatgrass (*Danthonia californica* Bol.), density in response to grazing and fire. They concluded that multiple year rainfall patterns can override grazing effects. We considered whether the season in which the fire occurred affected mortality and fecundity. Since we did not have observations from a fall fire during drought, this was not possible. A controlled experiment manipulating season, fire and rainfall regimes would likely provide more insight into these interactions and future studies focusing on *S. pulchra* mortality under fall drought conditions would be needed to quantify the relative effect of burn season and drought on *S. pulchra* responses.

Climate change is expected to increase fire frequency and significantly change rainfall patterns in southern California in the course of the next century (Sawyer et al. 2014). Non-native grasses are better adapted to those changes and are increasing in biomass (Lenihan et al. 2008), promoting drought through increased evapotranspiration in higher temperatures (Sandel and Dangremond 2012) and wildfire through an increase in fine flammable fuels that could further reduce the cover of perennial species (Keeley and Syphard 2019).

In order to mitigate climate change stress on native plant communities, it is important to consider the interaction of multiple factors acting on them. Large wildfires such as those experienced recently, and extended periods of drought are increasing (Sandel and Dangremond 2012; Keeley and Syphard 2019), thereby threatening native vegetation and

wildlife that are not able to adapt to the effects of climate change.

Conclusions

Under current climatic conditions, *S. pulchra*, is limited in its abilities to recover from the combined effects of fire and extended drought. The exceptional multi-year drought that California experienced from 2012 to 2016 caused an alarming mortality in many vegetation types, including those that are drought-adapted. Our results show that *S. pulchra* mortality was highest during drought and following a moderate-severity fire. Accordingly, fecundity and resprouting were lowest under those conditions. The combination of higher temperatures, more drought and more frequent fires creates novel environmental stress factors that may increase pressure on vulnerable ecosystems like native California grasslands. Future research should focus on experimentally testing the effects of multiple stress factors, possible mitigations to improve native grassland survival post-fire during drought, and the conditions under which attempting active restoration are most feasible. Finally, the Woolsey Fire that started on November 8, 2018, burned much of the land under examination in this study. This most recent wildfire in the SMMNRA can provide the opportunity to investigate post-fire recovery of *S. pulchra* after a year of above average precipitation.

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TWO NEW SPECIES OF *STREPTANTHUS* (BRASSICACEAE) IN SOUTHERN CALIFORNIA, AND NOTES ON THEIR CONSERVATION

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ABSTRACT

Herein I present the description of two new species, *Streptanthus medeirosii* N.Jensen from the Tehachapi Mountains in Kern County, and *S. juneae* N.Jensen from the San Bernardino Mountains in San Bernardino County, each described based on phylogenetic, morphological, geographical, and ecological evidence. In order to distinguish *S. medeirosii* and *S. juneae* from similar species, I provide diagnoses, a table comparing morphological characters, a taxonomic key, and maps showing their geographic ranges. To enable these comparisons, I also designate lectotypes for two closely related species, *S. bernardinus* (Greene) Parish and *S. campestris* S.Watson.

Key Words: Brassicaceae, endemic species, rare species, San Bernardino Mountains, southern California, *Streptanthus*, Tehachapi Mountains, Tejon Ranch.

It is widely recognized that current global extinction rates exceed historical background rates observed in the fossil record, and that Earth is in the midst of a sixth mass extinction (Pimm et al. 1995, 2014; Barnosky et al. 2011). Discovering and describing new species is central to understanding Earth's biodiversity and quantifying human impacts on that biodiversity (Costello et al. 2013). As much as 10 to 20 percent of plant species remain undescribed (Joppa et al. 2010). Pimm et al. (2014) conclude that there are currently around 400,000 documented plant species and that more than 50,000 plant species are yet to be described. The rate of description of new plant species has remained constant, at approximately 2000 new species per year between 1995 and 2015 (Christenhusz and Byng 2016). Even in North America, where efforts to catalog biodiversity exceed many other regions (Costello et al. 2013) and, in California, where botanical collecting efforts eclipse those in neighboring states (Taylor 2014), new plant species are discovered and described with regularity.

In 2013, I collected a perennial *Streptanthus* (Brassicaceae) on Tejon Ranch in the Tehachapi Mountains of Kern County that did not correspond to any described species based on morphological characters. Preliminary molecular phylogenetic analyses, using a single marker (nuclear ribosomal internal transcribed spacer region [nrITS], Jensen unpublished data) confirmed a close relationship between plants on Tejon Ranch and perennial *Streptanthus* in Southern California, including *S. bernardinus* (Greene) Parish and *S. campestris* S.Watson. Further fieldwork and continued phylogenetic research in Southern California uncovered a second undescribed species of *Streptanthus* in the San Bernardino Mountains. The evolutionary relationships of these two new species and related taxa are presented and discussed by Jensen (2018). Here, I

focus on describing these new species and contrasting them with closely-related species of *Streptanthus*.

Taxonomic and Phylogenetic Context

Streptanthus is a member of tribe Thelypodiaeae, sensu Prantl (1891), Al-Shehbaz (2012a), and Al-Shehbaz et al. (2006). Al-Shehbaz (2012a) placed 29 genera in Thelypodiaeae including (in California) *Streptanthus* Nutt., *Caulanthus* S. Watson, *Thelypodium* Endl., *Stanleya* Nutt., *Streptanthella* Rydb., and *Sibaropsis* S. Boyd & T.S. Ross. The placement of *Streptanthus* in Thelypodiaeae is not controversial, although circumscription of genera within the tribe has been in flux. Al-Shehbaz et al. (2006) hypothesized that the paucity of variation in molecular regions traditionally used for phylogenetic analysis (e.g., nrITS, cp *ndhF*) might be the result of recent and rapid diversification. Rapid radiation and whole genome duplication events have been cited as factors leading to difficulty in resolving relationships in Brassicaceae (Warwick et al. 2009; Franzkhe et al. 2011). Even so, Al-Shehbaz (2012a) expanded *Streptanthus* to include *Caulanthus*, *Guillenia* Greene, *Sibaropsis*, *Stanfordia* S.Watson and *Streptanthella*, among other genera, based on morphological evidence. Cacho et al. (2014) used three newly developed single-copy nuclear genes, three frequently used nuclear genes (ITS, *phyA*, PEPC), and two chloroplast regions (*trnL*, *trnH-psbA*) to provide the first significant insight into relationships among Thelypodiaeae. Their study focused on taxa native to California and included 143 accessions representing 46 of 53 species of *Streptanthus* and *Caulanthus*, plus samples of *Thelypodium*, *Stanleya*, and *Sibaropsis*. In contrast to previous studies, Cacho et al. (2014) recovered numerous clades in Thelypodiaeae and concluded that most currently recognized species

are monophyletic. However, neither *Streptanthus* in the strict sense nor *Streptanthus sensu* Al-Shehbaz (2012a) were inferred as monophyletic.

Cacho et al. (2014) recognized the Howellii Alliance, a clade of glabrous perennials with campanulate to tubular calyces, unfused filaments, and unkeeled sepals. The Howellii Alliance includes three species in northern California and southern Oregon (Northern Howellii Clade: *S. howellii* S.Watson, *S. longisiliquus* G.L.Clifton & R.E.Buck, and *S. barbatus* S.Watson), the widespread species, *S. cordatus* Nutt.; and two species in Southern California, *S. bernardinus* and *S. campestris* (Southern Howellii Clade). Evolutionary relationships inferred by Cacho et al. (2014) and Jensen (2018) are congruent. In both studies, the Howellii Alliance is monophyletic. The Northern Howellii Clade is sister to a clade containing *S. cordatus*, *S. oliganthus* Rollins and the Southern Howellii Clade. Clarifying relationships among the *S. howellii* Alliance was a major focus of Jensen (2018). These later results unambiguously support recognition of two new species in Southern California.

Species Delimitation in *Streptanthus*

A bewildering variety of traits has been used to differentiate species in *Streptanthus* and allied genera. Monographic studies focusing on *Streptanthella*, *Thelypodium* and *Caulanthus* (Payson 1922, Al-Shehbaz 1973) and North American Brassicaceae (Rollins 1993) helped to establish species boundaries in Thelypodiaeae. Treatments in recent floras by Al-Shehbaz (2005, 2012b) correspond with these classic works. It should be noted that, whereas generic delimitation of *Streptanthus* and allies have been in flux, the number of species and infraspecific taxa recognized in floristic treatments has changed little since the early 20th century. Recent phylogenetic research largely confirms historical species delimitations (Pepper and Norwood 2001; Bailey et al. 2006; Cacho et al. 2014; Jensen 2018). However, this research (Cacho et al. 2014, Jensen 2018) indicates that currently circumscribed genera, including *Caulanthus*, *Streptanthus*, and *Thelypodium*, are polyphyletic. This implies that, pending ongoing research, taxonomic changes will be necessary in the circumscription of these genera. It should be noted that the Howellii Alliance corresponds well to the genus, *Cartiera* Greene (Greene 1906). It may be appropriate to include taxa of the Howellii Alliance in *Cartiera* in the future.

Species in *Streptanthus* are generally distinguished from one another by a combination of vegetative, floral, fruit, and seed traits. For example, *S. longisiliquus* is diagnosed based on leaf shape, petal and sepal color, and fruit size and shape (Clifton and Buck 2007). *Streptanthus oblanceolatus* T.W.Nelson & J.P.Nelson is discerned from similar taxa based on filament fusion, presence of sterile anthers, leaf shape, sepal color, and fruit shape (Nelson and

Nelson 2009). *Streptanthus purpureus* Mata is differentiated from *S. polygaloides* A.Gray based on sepal and petal size, the presence of large seed wings, and seed coat ornamentation (Sanchez-Mata et al. 2013). As in many taxonomic groups, species delimitation in *Streptanthus* and allied genera is often based on suites of characters. Many of the characters used are reproductive (i.e., floral or fruit traits), but species descriptions rarely address whether newly described taxa are reproductively isolated from close relatives. Nonetheless, the differentiation of species in the genus often takes into account habitat and biogeography. For example, Clifton and Buck (2007) discuss morphology of northern Sierra Nevada endemic *S. longisiliquus* in reference to the morphologically similar *S. campestris*, *S. bernardinus*, and *S. cordatus*, only the latter is known to occur in Northern California. Within *Streptanthus* and related taxa, phylogenetic evidence (e.g., monophyly and lineage status) has not been used previously as evidence in the description of new species.

Herein I provide descriptions of two new species of *Streptanthus*. Morphological, phylogenetic, biogeographical and ecological data provide support for species recognition, consistent with the species concept outlined below. I provide a taxonomic key to perennial *Streptanthus* and *Caulanthus* in California, a table comparing species of *Streptanthus* in Southern California, and my perspective on morphological characters utilized in these identification resources. To facilitate this comparison, I have clarified the circumscription of *S. bernardinus* and *S. campestris* by designating lectotypes for these species. Lastly, I discuss the conservation status of *S. medeirosii* N. Jensen and *S. juneae* N. Jensen, as well as some taxonomic implications of ongoing molecular systematics research.

MATERIALS AND METHODS

Measurements used in the taxonomic treatments and keys below are derived from fresh field-collected material and dried specimens in herbaria. For the new species descriptions and for comparisons with *S. campestris* and *S. bernardinus*, I collected plant material from multiple populations of each species from 2013 through 2017. Measurements for floral and leaf characters were taken from fresh plant material. A comparison of fresh and dried material from the same collections indicates that floral and vegetative material typically shrinks five percent or less when dried. Measurements taken from dry plant material should take this into account. Seeds were collected from plants in the field or from herbarium specimens. Leaves and flowers were collected in the field from a minimum of 22 plants across the range of each taxon. Plant material was collected fresh and placed in a cooler with ice. Each evening, fresh flowers were dissected and mounted using double-stick tape. Floral dissections, fresh leaves, fruits and seeds were scanned in the field using a Canon 9000F

Mark II or at the Rancho Santa Ana Botanic Garden (RSABG) using an Epson Expression 10000XL scanner. Standard metric unit scales and color swatches were included on each scan to enable accurate measurements and assessment of color. Scans were imported into Image J (Schindelin et al. 2015), and measurements were calibrated to the metric scale for each scan using the “set scale” function. Plant height was measured in the field and from herbarium specimens. Calyx shape was evaluated based on observations and from photos taken in the field, as the three-dimensional nature of this important character is obscured or altered during the scanning process.

Herbarium specimens of *Streptanthus*, including types and original materials, deposited at CAS/DS, CHSC, DAV, DES, GH, MO, NDG, NY, RENO, RSA/POM, SBBG, SD, UC/JEPS, UCR and US were examined. Bibliographical citations in the original publications and databases, such as The International Plant Names Index (IPNI; <http://ipni.org/>), Tropicos (<http://www.tropicos.org/>), and The Plant List (<http://www.theplantlist.org/>) were also verified.

Species Concept Employed

Mayr (1996) defines species as groups of populations that are “isolated from each other” resulting in the “integrity of their genotypes.” This principle is fundamental to the biological species concept in which species are reproductively isolated from one another (Mayr 2000). The challenge in applying the biological species concept universally across the tree of life has contributed, at least in part, to a proliferation of alternative species concepts; from those based solely on molecular evidence to those relying entirely on morphological evidence (as reviewed in Mayden 1997, Wheeler and Meier 2000, de Quieroz 2007). In an attempt to find consensus among sometimes disparate concepts, de Quieroz (2007) proposed a Unified Species Concept in which species are defined as “separately evolving metapopulation lineages.” Critics have argued that the presence of a distinct lineage is not sufficient evidence to support delimitation of a species (Freudenstein et al. 2016). They advocate that phenotypic aspects of a lineage such as morphology, phenology, and ecological role should be used in concert with (and even weighted over) molecular evidence to delimit species.

I employ a species concept that utilizes multiple lines of evidence to delimit new species in *Streptanthus*, which is consistent with both de Quieroz (2007) and Freudenstein et al. (2016). New species in *Streptanthus* are lineages distinct from previously described species. These new lineages are cohesive from a molecular perspective and supported by various phylogenetic methods (Jensen 2018). New species are also morphologically cohesive and distinguishable from previously described species. Lastly, I incorporate biogeographical evidence drawing from the known ranges of described species and ecological

and phenological evidence, where applicable. I surmise that the sum of multiple lines of evidence is ample justification for the recognition of these new species.

TAXONOMIC TREATMENT

Lectotypification of Southern California Perennial *Streptanthus*

***Streptanthus campestris* S.Watson**, Proceedings of the American Academy of Arts and Sciences 25:125. 1890.—Type (syntypes): USA. CALIFORNIA. San Diego Co. “At Campo, near the southern boundary of California: George R. Vasey (Vasey 26, June 1880, GH00422106!, GH00286769!, US00099811!) and S. G. (sic) Parish (Parish and Parish 449, June 1880, GH00061149!) in 1880. A specimen collected by the latter in the San Bernardino Mountains is apparently the same.” The latter specimen has not been found. Lectotype (here designated): GH00061149! S. B. Parish and W. F. Parish 449, USA, California, San Diego County, near Campo, June 1880.

The earliest known southern California collections of *Streptanthus* were those of G. R. Vasey, S. B. Parish and W. F. Parish in 1880 (GH00422106, GH00286769, US00099811, GH00061149), near Campo (ca. 2 km north of the Mexican border), San Diego County. These collections represent what is now referred to as *Streptanthus campestris* S.Watson. In 1881, S. B. Parish and W. F. Parish apparently returned to the area (Parish and Parish 446, June 1881; CAS-BOT-BC61189) making additional collections. The Parish brothers made extensive collections in the San Bernardino Mountains of San Bernardino Co., California and in 1881 they collected what is now referred to as *S. bernardinus* (Greene) Parish there (Parish and Parish 1094 GH379973). In 1884, they made subsequent collections of *Streptanthus* in the San Bernardino Mountains under the same catalog number (Parish and Parish 446, August 1884, CAS-BOT-BC61195, UC118539; Parish and Parish 446, August 1885, UC187982). As a consequence of these early collections, Sereno Watson described *S. campestris* in 1890. However, as noted above, these collections represent two relatively distinct species.

To be consistent with the current application of the name *S. campestris* and also with the intended lectotypification of Roy Buck (annotation on GH00061149), I select a specimen collected by the Parish brothers in 1880, near Campo, GH00061149.

***Streptanthus bernardinus* (Greene) Parish**, Plant World 20:216. 1917. Basionym: *Agianthus bernardinus* Greene Leafl. Bot. Observ. Crit. 1: 228. 1906.—Type (syntypes): USA, CALIFORNIA, San Bernardino Co. “San Bernardino Mountains, Parish (S. B. Parish 3753 GH379975!, US1898311!, US268217!,

CAS-BOT-BC61196 [CAS76482], UC10866); also, San Jacinto Mountains, H. M. Hall (possibly *H. M. Hall* 2243 CAS-BOT-BC61183 [DS42837], UC10865, *H. M. Hall* 2660 UC117803, *H. M. Hall* 2661 UC117803)." Lectotype (here designated): US1898311!, S.B. Parish 3753. USA, San Bernardino County, California, San Bernardino Mountains, Bear Valley, June 16, 1895. Isolectotypes: CAS76482!, UC10866, GH379975!, US268217!.

Streptanthus bernardinus was described by Greene (1906) under the basionym *Agianthus bernardinus*. He cites the locations and collectors of syntypes as, "San Bernardino Mountains, Parish also San Jacinto Mountain, H.M. Hall." Parish created a new combination transferring *A. bernardinus* Greene into *Streptanthus*. A considerable number of collections of *S. bernardinus* were made by Parish in the San Bernardino Mountains. These include *S.B. Parish and W.F. Parish* 446A (UC118539, UC187982, CAS-BOT-BC61195), *S.B. Parish and W.F. Parish* 1094 (GH379973), *S.B. Parish* 3035 (RSA429515, UC11744, MO100292109), and *S.B. Parish* 3753 (CAS-BOT-BC61196 [CAS76482], GH379975, UC10866, US1898311, US268217). It is not evident from the protologue if more than one collection was the basis for *A. bernardinus*. No specimens of *A. bernardinus* are found at ND-G (B. Helenthal, Greene-Nieuwland Herbarium, personal communication); however, Greene was at the Smithsonian Institution between 1904 and 1915, making US an obvious herbarium for the type specimens to reside. Two sheets are filed with the name "*Agianthus bernardinus* Greene, Isotype" (not in Greene's handwriting), US1898311 and US268217, collected by Parish (3753). As noted above, this collection is also represented in GH and CAS. At MO, one sheet is identified as the isolectotype (*S. B. Parish* 3035, 25 June 1894, MO19225591/BC:MO-2196087). The collection number of this specimen does not correspond with those which have been identified as isotypes at US.

Collections made by H. M. Hall in the San Jacinto Mountains are also syntypes; however, there are three collections made in 1901: *H. M. Hall* 2243 (CAS-BOT-BC61183 [DS42837], UC10865), *H. M. Hall* 2660 (UC117803), *H. M. Hall* 2661 (UC117803). None of these collections are found at US. Thus, it is not clear which (if any) of these collections were observed by Greene or used in producing the protologue. I am confident that the specimens at US were used by Greene and therefore consider *S. B. Parish* 3035 original material. The specimen most closely matching the protologue is US1898311 (BC: 00099809).

New Species Descriptions

Streptanthus medeirosii N.Jensen, sp. nov. (Figs. 1, 2A–C).—Type: USA. CALIFORNIA. Kern Co.,

Tejon Ranch, Tehachapi Mountains, Blue Ridge, 34.925716°, -118.648578°, 26 June 2014, N. Jensen 2419 (holotype: RSA; isotypes: UC, US).

Plants perennial, glabrous, glaucous 24–50 cm (mean: 36 cm, SD: 8.4 cm) tall, dying back to a branched woody caudex in the late fall. **Roots** fibrous, rhizomes absent. **Stems** ascending, branched only at base. **Basal leaves** numerous, alternate, often glaucous, light gray green to dark green, surface dull to shiny; petioles usually distinct proximally, cuneate, with narrow laminar tissue gradually increasing in width and transitioning into blade, sometimes with prominent wing making transition between blade and petiole indistinct, 4–26 mm (mean: 10.4 mm, SD: 5.3 mm); blades coriaceous, thick, obovate to spatulate, 22–82 mm (mean: 55.5 mm, SD: 13.3 mm) long by 13–33 mm (mean 23 mm, SD: 4.5 mm) wide; apices obtuse to acute; margins sometimes entire, often with only a few teeth at apex, or entire proximally and prominently dentate on distal margins and at the apex. **Cauline leaves** alternate, often glaucous, light gray green to dark green, surface dull to shiny; petioles absent; blades reniform to amplexicaul at base, obtuse to acute at apex, coriaceous at maturity, thick, obovate to lanceolate or narrowly elliptic, 24–64 mm (mean: 46 mm, SD: 12) long by 7–27 mm (mean: 16 mm, SD: 5) wide, gradually reduced in size distally; margins entire, or with a few teeth at apices. **Inflorescences** indeterminate, racemose, ebracteate, cluster of sterile flowers at apices absent, flowers numerous. **Pedicels** erect, 1.3–4.2 mm (mean: 2.4 mm, SD: 0.7 mm). **Calyces** campanulate, inflated basally, outer sepals often not overlapping inner sepals. **Sepals** four, free to base, elliptic to ovate (inner slightly smaller, usually elliptic), 5.1–7.7 mm (mean: 6.5 mm, SD: 0.62 mm) long by 2.2–5.3 mm (mean: 3.5 mm, SD: 0.66 mm), not keeled, trichomes usually absent, but occasionally a few present apically, light green to white to cream basally, tips usually green, sometimes purple with age; apices rounded to obtuse; bases rounded to truncate; margins entire, hyaline and transparent or tinged pink. **Petals** four, free to base, narrowly elliptic to narrowly oblong with or without a distinct widened area (limb) near the middle, 6.6–10.4 mm (mean: 8.5 mm, SD: 0.85 mm) long by 1.2–2.7 mm (mean: 2.0 mm, SD: 0.33 mm) wide, bases light green to cream, tips maroon to dark purple, veins prominent at mid-petal; apices acute, exserted from calyx, reflexed; bases truncate to rounded; margins entire, not crisped. **Stamens** six, in pairs of 3 unequal lengths resulting from differences in filament elongation. **Filaments** six, free to base; adaxial (longest) pair 4.4–7.2 mm (mean: 5.9 mm, SD: 0.87 mm) long; abaxial (shortest) pair 3.1–6.6 mm (mean: 4.9 mm; SD: 0.99 mm) long; lateral pair 2.3–6.4 mm (mean: 4.2, SD: 0.98 mm) long. **Anthers** six, all fertile, dehiscing in pairs asynchronously first on the adaxial stamen pair and last on the abaxial pair, 2.3–4.2 mm (mean: 3.1 mm, SD: 0.52 mm) long at anthesis, length of each

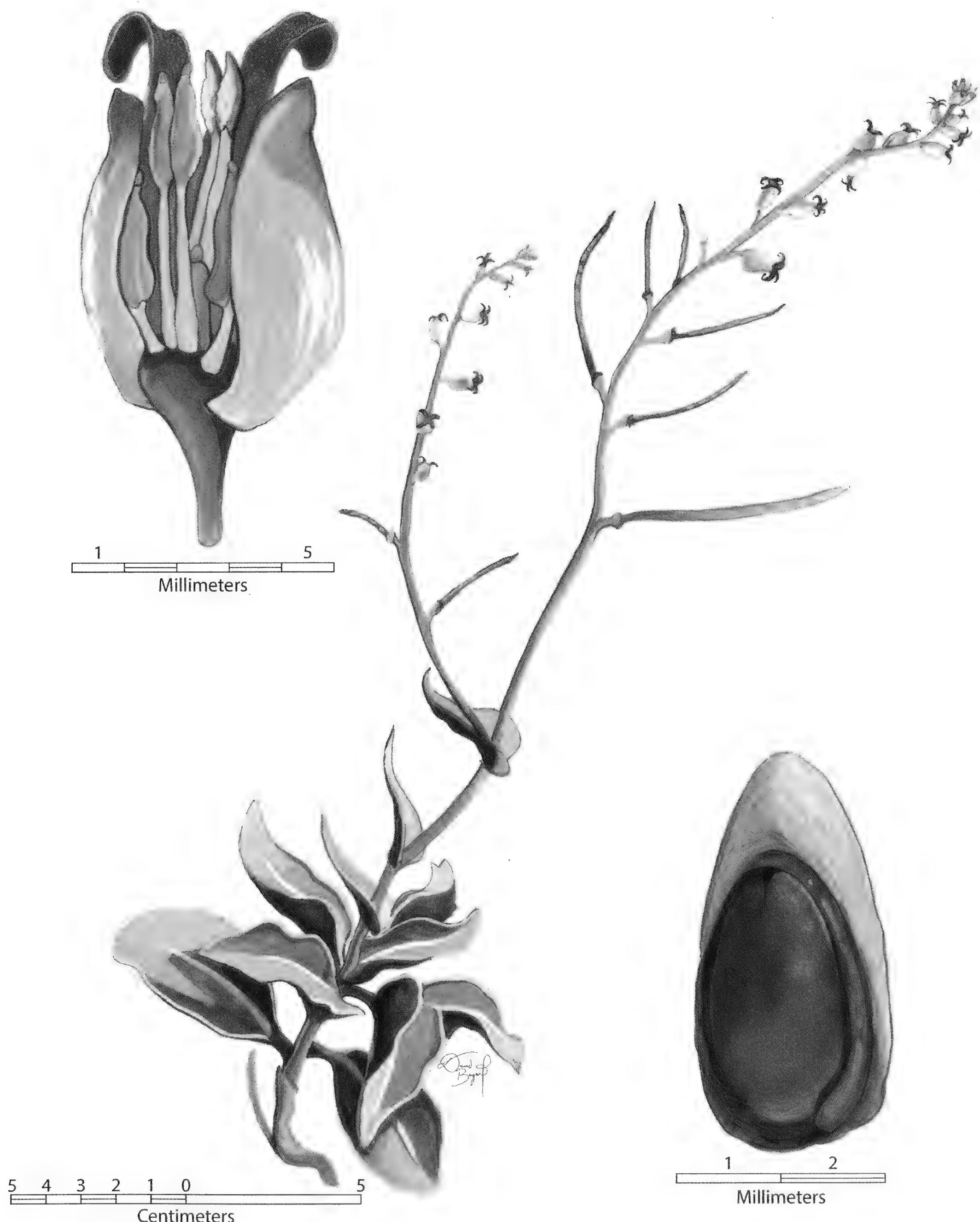
Streptanthus medeirosii N. Jensen

FIG. 1. Illustration of *S. medeirosii*. A. Entire plant showing growth habit, leaves, flowers and fruits. B. Single flower with one sepal removed to show reproductive parts. C. Single seed, the lighter portion at the bottom of the seed is the seed wing. Illustration by David Bryant.



FIG. 2. Photos of *S. medeirosii* and *S. juneae*. A. Flowers of *S. medeirosii*. B. Entire plant of *S. medeirosii*. C. Habitat of *S. medeirosii*. D. Flowers of *S. juneae* and flora visitor, *Osmia* sp. (Family Megachilidae). E-Flower of *S. juneae*. F-Entire plant of *S. juneae*. Photo credits A, B: Chris Winchell; rest: Nick Jensen.

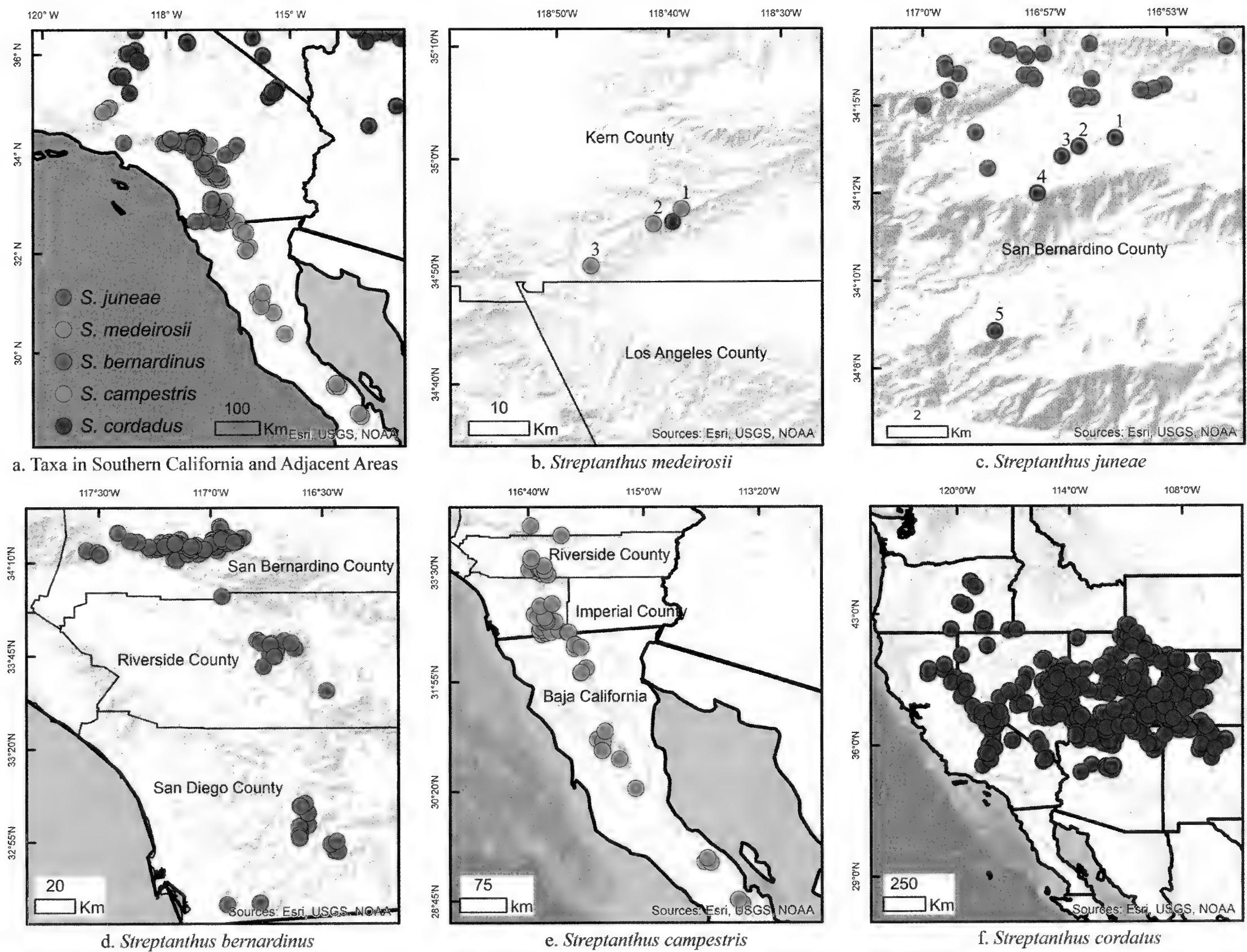


FIG. 3. The distribution of species of perennial *Streptanthus* in Southern California and adjacent areas. State/province boundaries and county lines, when appropriate, are shown. A. The Howellii Alliance in Southern California and adjacent areas of Arizona, Nevada and Baja California, MX, including *S. juneae*, *S. medeirosii*, *S. bernardinus*, *S. campestris*, and *S. cordatus*. B. Map detailing the range of *S. medeirosii* (red), numbers correspond to the locations referred to in the discussion of conservation status. A single location of *S. cordatus* is shown (green). C. The range of *S. juneae* (purple), numbers correspond to the locations referred to in the discussion of conservation status. Numerous locations of *S. bernardinus* (light green) are visible to the north. D. The range of *S. bernardinus* (light green), locations of *S. campestris* and *S. juneae* not shown. E. Distribution of *S. campestris* (yellow), locations of *S. juneae* and *S. bernardinus* not shown. F. The range of *S. cordatus* (dark green). Other taxa not shown. Data Source: Consortium of California Herbaria (2017).

pair unequal. **Gynophores** 0.36–0.86 mm (mean: 0.59 mm, SD: 0.13 mm) long in fruit. **Ovaries** superior, bicarpellate, syncarpous, with two carpels (valves) separated by a straight, entire replum; stigma entire; ovules 16–32 (mean: 24, SD: 4.5) per ovary, half in each valve. **Fruits** siliques, dehiscent at maturity, flattened, outer walls of valves smooth, not constricted between seeds, erect to arched, 55–104 mm (mean: 78 mm, SD: 13 mm) long by 2.4–4.1 mm (mean: 3.1, SD: .36 mm). Style in fruit 1.6–3.8 mm (mean: 2.2 mm, SD: 0.62 mm) long. **Seeds** oblong to ovate, dark brown to black, 3.3–4.4 mm (including wing; mean: 3.8 mm, SD: 0.28 mm) by 2.0–2.7 mm (mean: 2.3 mm, SD: 0.15 mm) wide; wings not continuous in width around margin, often absent at base and on sides, prominent apically, 0.38–1.24 mm (mean: 0.62 mm, SD: 0.18 mm) wide apically, 0–0.38 mm (mean: 0.09 mm, SD: 0.08 mm) wide laterally.

Large wings at the apices of seeds distinguish *Streptanthus medeirosii* from all other perennial *Streptanthus*. *Streptanthus medeirosii* occurs in the Tehachapi Mountains in close proximity to *S. cordatus* (Fig. 3B), but is distinguishable from *S. cordatus* by its strongly campanulate calyces that are inflated at the base, sepals lacking purple pigmentation, and entire to sparsely dentate basal leaves. *Streptanthus cordatus* in the Tehachapi Mountains has calyces that are not nearly as inflated proximally, sepals that are typically tinged pink to purple apically or are entirely pink to purple, basal leaves with uniformly deeply dentate margins, and smaller seed wings. *Streptanthus cordatus* has wider fruits than *S. medeirosii*. Fruits in *S. cordatus* typically exceed 3 mm in width and bear prominent thickened margins and prominent midveins. *Streptanthus medeirosii* is distinguished from *S. bernardinus* by its purple petal tips, sepals that are occasionally tinged pink, and

calyces that are not nearly as strongly inflated. *Streptanthus bernardinus* has calyxes that are prominently inflated, especially at the base, and petals lacking purple pigmentation. *Streptanthus medeirosii* is distinguished from *S. juneae* by its more upright, wider fruits, inflated calyx bases, and sepals that typically lack purple pigmentation. *Streptanthus campestris* is distinguished from *S. medeirosii* based on clusters of dark purple flowers at inflorescence apices, ciliate petiole margins, and plant height often exceeding 1 m. The documented range of *S. medeirosii* does not overlap with *S. bernardinus*, *S. campestris* or *S. juneae*.

Paratypes. USA, CALIFORNIA, Kern Co.: Tejon Ranch, Tehachapi Mountains, 6 June 2007, *Leager* s.n. (UCR251770); Tejon Ranch, Tehachapi Mountains, Blue Ridge 31 July 2013, *Jensen* 524 (RSA, UC); Tejon Ranch, Tehachapi Mountains, Blue Ridge, 13 June 2017, *Jensen* 4764 (RSA, UC, US).

Etymology. This species commemorates my friend and mentor, Joe Medeiros. I met Joe when I was a student at Sierra College in Rocklin, CA, where he taught botany for many years. He encouraged me to study botany and ignited not only my passion for the flora of California, but also to fight for its conservation. Recommended common name: Tejon jewelflower.

Distribution and ecology. The range of *Streptanthus medeirosii* is restricted to the Tehachapi Mountains in Kern County of Southern California, where it is known from three locations on Tejon Ranch (Fig. 3B).

Streptanthus medeirosii begins flowering in early June. Flowering extends into early September and fruit set occurs from July through September. Phenology, however, is variable and governed by weather conditions. For example, I first collected *S. medeirosii* in full flower on the last day of August 2013. In contrast, plants had nearly finished flowering by early August in 2017. Plants die back completely to a woody caudex each winter and are not detectable during dormancy; they resume vegetative growth in the late-spring.

Streptanthus medeirosii grows on steep north or east-facing slopes with exposed, unstable rocks of carbonate or granitic origin. It also occurs in cracks on rock outcrops along a road cut. These habitat conditions in the Tehachapi Mountains are occupied by forest dominated by *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr., *Quercus wislizeni* A. D.C. var. *wislizeni*, *Q. chrysolepis* Liebm., *Q. kelloggii* Newb., or a combination of these taxa. *Streptanthus medeirosii* occurs in the shade or in sunny openings where herbaceous and shrub cover is sparse. Associated taxa include *Hosackia crassifolia* Benth. var. *crassifolia*, *Nicotiana attenuata* Torr. ex S.Watson., *Eriogonum nudum* Benth. var. *pauciflorum* S.Watson, *E. roseum* Durand & Hild., *Chenopodium fremontii* S.Watson, *Sambucus nigra* L. subsp. *caerulea* (Raf.) Bolli, *Penstemon grinnellii* Eastw., *Erysimum capitatum* (Douglas ex Hook.)

Greene, *Bromus diandrus* Roth, *Phacelia ramosissima* Douglas ex. Lehm., *Mentzelia albicaulis* (Douglas ex Hook.) Douglas ex Torr. & A.Gray, and *Sisymbrium orientale* L. Flowers of *S. medeirosii* are frequently visited by native bees, including *Bombus* spp. (Jensen, personal observations). Plants occur over an elevation range of 1600 to 1850 m.

Streptanthus juneae N.Jensen, sp. nov. (Figs. 2D–F, 4).—Type: USA, CALIFORNIA, San Bernardino Co., San Bernardino Mountains, south of Big Bear Lake, 34.235587° , -116.905655° , 17 June 2017, N. Jensen 4773, S. Namoff, J. Orozco, J. Kitchens, B. Connally (holotype: RSA; isotypes: UC, US, CAS, UCR, MO).

Plants perennial, glabrous, 22–56 cm (mean: 36 cm, SD: 10 cm), dying back to a woody caudex following the growing season. **Roots** fibrous, rhizomes absent. **Stems** ascending, sometimes growing rhizome-like just below the soil surface for up to 20 cm with one to two stems emerging per year, solitary or branched up to three times from the base or occasionally at mid-stem below inflorescence. **Basal leaves** numerous, alternate, light gray green to dark green, surface dull; petioles usually distinct at least proximally, cuneate, most unwinged, but some with wings making the distinction between petiole and blade difficult, 6.6–35.4 mm (mean: 14.7 mm, SD: 4.8 mm); blades coriaceous, thick, ovate to lance-ovate to spatulate, apices acute to obtuse, often mucronulate, 35.6–104 mm (mean: 49.6 mm, SD: 12.7 mm) long by 9.2–34.8 mm (mean: 15.5 mm, SD: 4.5 mm) wide.; margins sparsely serrate to dentate, rarely entire. **Cauline leaves** alternate, light green to gray green, surface dull; petioles absent; blades coriaceous, thick, lanceolate to lance-ovate to triangular, bases reniform to amplexicaul, 26–59 mm (mean: 41 mm, SD: 10 mm) long by 6.2–23 mm (mean: 11.6 mm, SD: 3.6 mm) wide, gradually reduced in size distally; apices acute to obtuse; margins often entire, occasionally sparsely dentate to serrate. **Inflorescences** indeterminant, racemose, ebracteate, sterile cluster of flowers at apices absent, flowers numerous. **Pedicels** erect to arched, 5.2–11.5 mm (mean: 7.6 mm, SD: 1.8 mm). **Calyces** tubular to narrowly campanulate. **Sepals** four, free to base, obovate to oblanceolate (inner pair slightly smaller than outer), apices rounded to obtuse, bases rounded to truncate, 5.2–9.0 mm (mean: 6.9 mm, SD: 0.9 mm) long by 1.4–3.5 mm (mean: 2.4 mm, SD: 0.4 mm), not keeled, trichomes at apices absent, green, tinged pink in bud, green tinged pink to universally light purple, darkest along margins, rarely only green; margins entire, hyaline, often tinged pink, sometimes transparent. **Petals** four, free to base, narrowly elliptic, rarely with differentiated into widened blade near middle, 7.0–12.3 mm (mean: 9.6, SD: 1.0 mm) long by 0.64–2.6 mm (mean: 1.4, SD: 0.45) wide, bases light green to yellow, distal quarter to half dark purple, midvein occasionally visible, lateral veins not visible; apices acute, exserted from the calyx, erect to slightly reflexed; bases

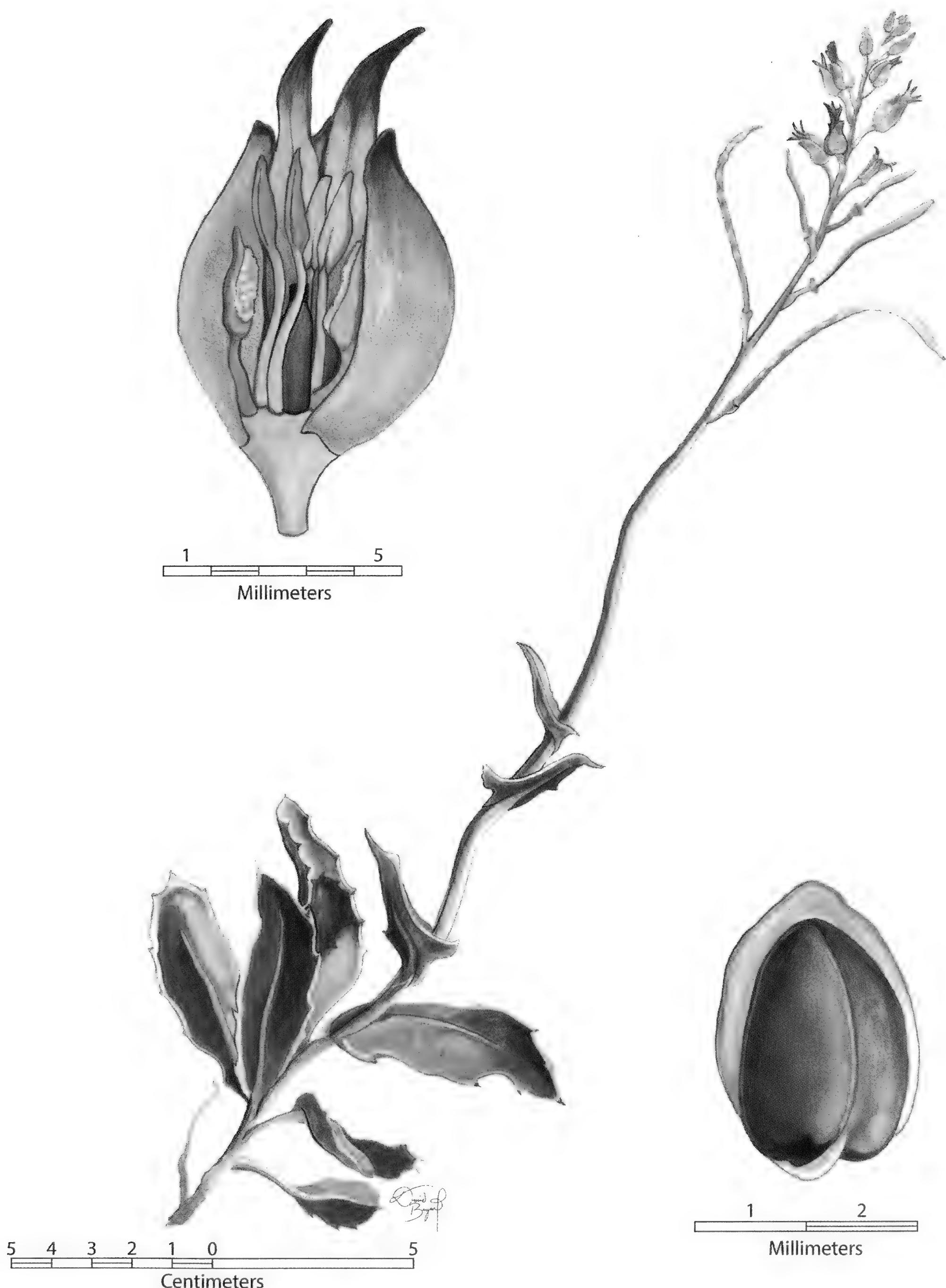
Streptanthus juneae N. Jensen

FIG. 4. Illustration of *S. juneae*. A. Entire plant showing growth habit, leaves, flowers and fruits. B. Single flower with one sepal removed to show reproductive parts. C. Single seed, the lighter portion at the bottom of the seed is the seed wing. Illustration by David Bryant.

truncate to rounded; margins entire, not crisped. **Stamens** six, in pairs of 3 unequal lengths owing to differences in filament elongation. **Filaments** six, free to base; adaxial (longest) pair 2.5–7.0 mm (mean: 5.1 mm, SD: 1.1 mm) long; abaxial (shortest) pair 2.3–6.2 mm (mean: 4.2 mm, SD: 1.1 mm) long; lateral (medium) pair 1.6–6.0 mm (mean: 3.2 mm, SD 1.1 mm) long. **Anthers** six, all fertile, dehiscing in pairs asynchronously first on the adaxial stamen pair and last on the abaxial pair, 2.3–6.2 mm (mean: 4.2 mm, SD: 1.1 mm) long at anthesis. **Gynophores** 0.47–0.98 mm (mean: 0.69 mm, SD: 0.12 mm) long in fruit. **Ovaries** superior, bicarpellate, syncarpous, with two carpels (valves) separated by a straight, entire replum; stigma entire; ovules 30–50 (mean: 40, SD: 6) per ovary, with half occurring in each valve. **Fruits** siliques, dehiscent at maturity, flattened, outer walls of valves smooth, not constricted between seeds, arched to occasionally erect, 73–141 mm (mean: 108 mm, SD: 16 mm) long by 1.6–3.2 mm (mean: 2.4 mm, SD: 0.40 mm) wide. Style in fruit 1.4–3.7 mm (mean: 2.5 mm, SD: 0.57 mm) long. **Seeds** elliptic, light to dark brown, including wing 1.4–3.7 mm (mean: 2.5 mm, SD: 0.57 mm) by 1.8–2.1 mm (mean: 2.0 mm, SD: 0.70 mm) wide; wings sometimes continuous, often absent or nearly so on sides, present on apices, 0.12–0.51 mm (mean: 0.30 mm, SD: 0.11) wide at tip, 0–0.27 mm (mean: 0.19 mm, SD: 0.044 mm) on sides.

Streptanthus juneae grows within five km of extant populations of *S. bernardinus* and within 25 km of *S. campestris*. *Streptanthus bernardinus* has petals that are white or cream colored, rarely yellow to very light orange apically, and sepals that are white to green-colored and very inflated at their bases. *Streptanthus juneae* has petals that are dark purple distally and calyces that are scarcely inflated at the base to tubular in shape, and sepals that are tinged purple or pink at least at their tips, especially in age. The range of *S. campestris* extends south from the southeastern foothills of the San Bernardino Mountains, south to the mountains of Baja California, Mexico. A single historical collection, *McGregor* 57 (DS300566), from Pipes Canyon in the Little San Bernardino Mountains is morphologically most similar to *S. campestris*. *Streptanthus campestris* has a cluster of fertile flowers with dark purple calyces at the apex of each inflorescence. Calyces in this species are almost always uniformly dark purple. *Streptanthus campestris* is much taller than *S. juneae* with plants often exceeding one m in height. Leaves in *S. campestris* are larger and are thin and papery (especially when dry), in contrast to the smaller, coriaceous leaves of *S. juneae*. *Streptanthus campestris* is most often found in dry washes in the understory of oak woodland habitats in the transition zone between montane and desert habitats. *Streptanthus juneae* is a plant of montane conifer forest and chaparral habitats. The two species are also separated phenologically, with *S. campestris* typically flowering much earlier than *S. juneae*. *Streptanthus cordatus* and *S. medeirosii* are distinguished from *S. juneae* based on

their wider, erect fruits. The ranges of *S. cordatus* and *S. medeirosii* do not overlap with the ranges of *S. juneae*, *S. bernardinus*, or *S. campestris*.

Paratypes. USA, CALIFORNIA, San Bernardino Co., San Bernardino Mountains: Bluff Lake, July 1899, Hall. s.n. (JEPS27097); San Bernardino Peak trail from Glen Martin, 22 July 1925, Feudge 1107 (POM98754); head of Clark's Grade, 1 July 1926, Munz 10577 (POM96794); San Bernardino Peak trail from Glen Martin, 16 August 1953, Howe s.n. (SD45582); head of Clark's Grade, 17 August 2010, Stoughton 582 (UCR238715); south of Big Bear Lake, 28 June 2015, Jensen 3874 (CAS, RSA, UC, US); head of Clark's Grade, 29 June 2015, Jensen 3875 (RSA, UC, US); Pine Knot Trail, 17 June 2017, Jensen 4772 (RSA, UC, US, UCR); along Mill Creek Road, 18 June 2017, Jensen 4774 (RSA, UC).

Etymology. This species is named after my grandmother, June Jensen. When I was very young she introduced me to the joy of growing plants, sparked my curiosity in the natural world, and has remained an inspiration throughout my life. *Streptanthus juneae* can be observed in full flower in the month of June. Recommended common name: June's jewelflower.

Distribution and ecology. The entire known range of *S. juneae* is within the San Bernardino Mountains of San Bernardino County, where it is known from five locations spanning a linear extent of approximately 13 km (Fig. 3C). The farthest west location is near Glen Martin on the trail to Mount San Bernardino and the farthest east location is near Knickerbocker Lane south of Big Bear Lake.

Streptanthus juneae begins flowering in early June and continues flowering into August. Fruit set begins in late June and continues into September, with fruits dehiscing in late September. Plants die back to a woody caudex with the onset of winter and are not easily detectable until growth resumes in May and June.

Streptanthus juneae typically grows on moderate slopes with varying aspects to flat areas in the understory of open forest habitat dominated by *Pinus jeffreyi* Grev. & Balf., *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr., and *Quercus kelloggii* Newb. The population at Clark's Grade is found in openings in montane chaparral dominated by *Ceanothus cordulatus* Kellogg resulting from recent logging activity. Plants are found on loose, sandy or gravelly substrates of granitic origin, often in the proximity of large granitic boulders. Plants growing in proximity to conifers often are found in thick duff composed of pine needles. Associated taxa include *Bromus tectorum* L., *Penstemon grinnellii* Eastw., *P. rostriflorus* Kellogg, *Elymus glaucus* Buckley, *E. elymoides* (Raf.) Swezy, *Poa secunda* J.Presl, *Eriogonum* spp., *Gayophytum diffusum* Torr. & A.Gray subsp. *parviflorum* H.Lewis & Szweyk., and *Ericameria nauseosa* (Pursh) G.L.Nesom & G.I.Baird. Flowers of *S. juneae* are frequently

2020 Annual Banquet and Meeting
April 4, 2020
UC Santa Cruz Arboretum & Botanic Garden
CANCELLED

March 13, 2020

Dear Friends and Colleagues of the California Botanical Society,

With a heavy heart (but with lots of company), due to the COVID-19 pandemic, the Council of the California Botanical Society has decided to cancel the upcoming annual banquet, which was to have taken place on Saturday, April 4, 2020, at the UC Santa Cruz Arboretum. We hope that you, your families, and friends (and, well, *everyone*) all stay well during this unpredictable time.

The Society extends our warmest appreciation to Brett Hall, the Arboretum's California Native Plant Program Director, who organized the banquet this year. Brett did an incredible job over the last few months, reserving the venue, hiring the caterer, organizing the field trips and Arboretum tours, and, especially, catalyzing the recent rains, which were destined to promote excellent wildflower-viewing! We were also greatly looking forward to a reception in honor of **Professor Emeritus** (and botanical trailblazer) **Jean Langenheim** and to the after-dinner talk on *The evolution of serpentine specialists and generalists*, by UC Santa Cruz **Professor Kathleen Kay**.

Excellent (mitigating) news is that Brett has offered to be the organizer and host for next year's California Botanical Society Graduate Symposium, along with its evening banquet, both to be held at UC Santa Cruz. So...please be on the look out for future announcements of what we anticipate will be the Society's next Great Event.

As always, the Council greatly appreciates your membership in the Society, and we are always eager to hear your suggestions for ways in which we may more deeply engage western U.S. botanists in fulfilling our collective goals and aspirations. Please don't hesitate to contact me with any questions or suggestions.

Sincerely,

Susan J. Mazer

President, California Botanical Society
Professor of Ecology and Evolution
Department of Ecology, Evolution and Marine Biology
University of California, Santa Barbara
Email: sjmazer@ucsb.edu



Torreya californica
Swanton,
North coast Santa Cruz
All photos: Brett Hall

Lupinus albifrons,
Bonny Doon
Ecological Reserve

Hosackia gracilis,
Upper Marshall Fields

Paul Silva Student Research Grants

Deadline: May 15, 2020

The Paul Silva Student Research Grant is named after Paul Silva (1922-2014), a phycologist and Curator of Algae at the University Herbarium, UC Berkeley, whose bequest to the Society has made this award possible. Awards are made to qualified undergraduate and graduate student members of the Society working on projects that will help achieve the Society's goal of advancing Western American botany. Students from any accredited university doing botanical research within western North America and who are members of the Society are eligible for this award.

Proposals will be reviewed by a panel of experts, and winners will be announced within two months of the application deadline.

For application details and an application form, as well as previous grant recipients, please go to calbotsoc.org/grants/#PaulSilva

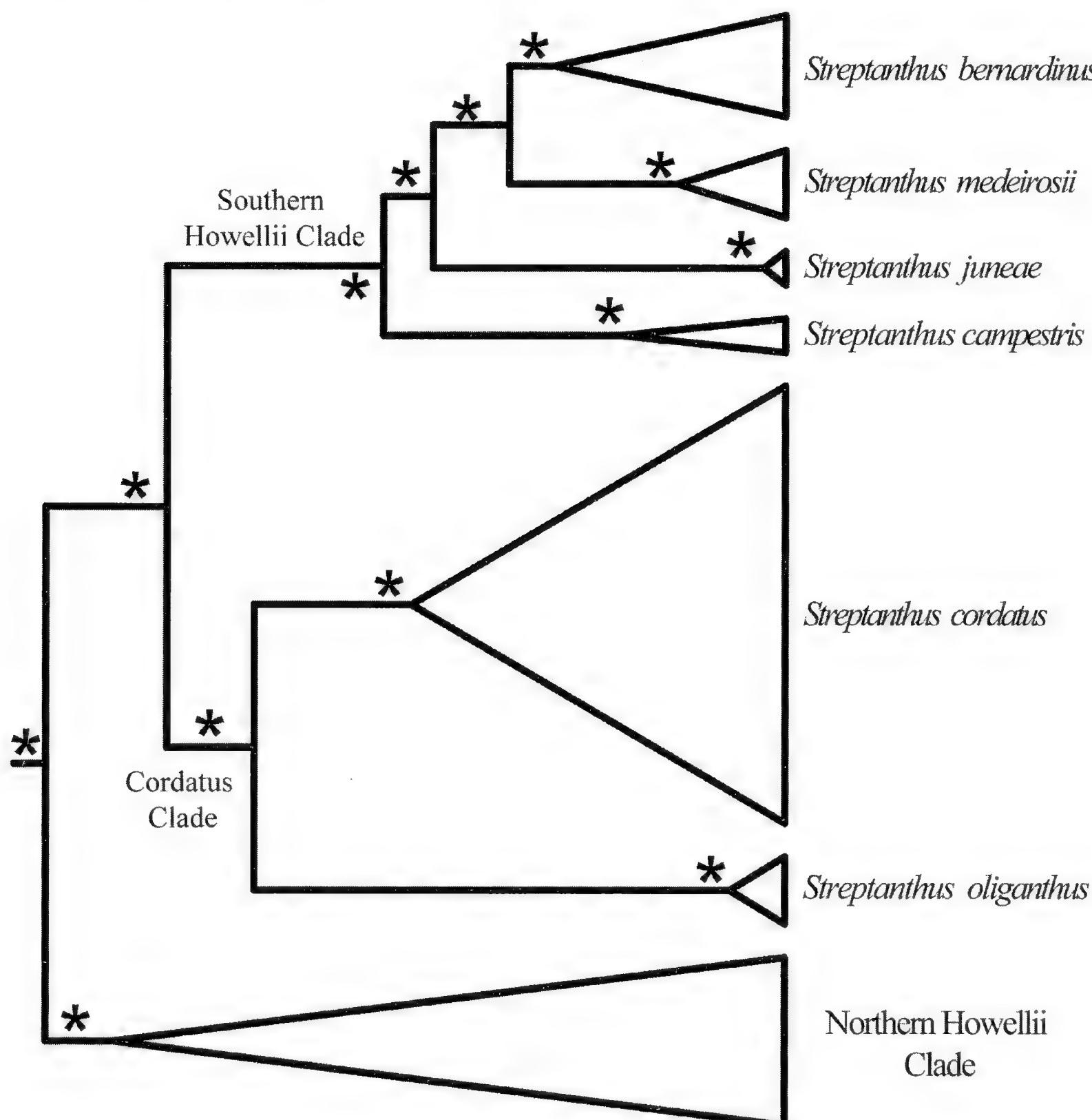


FIG. 5. Phylogeny depicting evolutionary relationships in species of *Streptanthus* in the Howellii Alliance. For more information on phylogenetics in *Streptanthus* see Jensen (2018). Asterisks (*) indicate a Bayesian posterior probability value of 1 and maximum likelihood bootstrap support of 100.

visited by native bees. In particular, *Osmia* sp. (Family Megachilidae) were observed repeatedly visiting numerous flowers in several populations of *S. juneae* in June 2017 (Fig. 2D). It occurs over an elevation range of 1980 to 2370 m.

DISCUSSION

Evolutionary Relationships and Taxonomic Decisions

Investigation into the phylogenetic relationships in the Howellii Alliance (Fig. 5, from Jensen 2018), confirms the placement of *S. medeirosii* and *S. juneae* within a clade of perennial *Streptanthus* of southern California and Baja California, Mexico (the Southern Howellii Clade). In addition to the two new species, this clade includes *S. bernardinus* and *S. campestris*. Analyses using BEAST2 (Bouckaert et al. 2014) and RAxML (Stamatakis 2014) support a sister relationship between *S. medeirosii* and *S. bernardinus* with *S. juneae* sister to that clade, and *S. campestris* sister to these three species (Jensen 2018). A clade containing *S. cordatus* and *S. oliganthus* is sister the Southern Howellii Clade.

The clade containing perennial *Streptanthus* in northern California (the Northern Howellii Clade) is sister to the *S. cordatus* + Southern California clades. All evolutionary relationships in the Howellii Alliance are supported by Bayesian posterior probability support values of 1 and Maximum Likelihood bootstrap support values of 100. All four Southern California taxa are also relatively easy to distinguish morphologically, especially in conjunction with biogeographic and ecological evidence (see dichotomous key and Table 1).

Habitat Within an Evolutionary Context

Recent research indicates that many species of *Streptanthus* occupy open, bare habitats (Cacho and Strauss 2014), and that the occupation of these types of habitats may be a precursor to edaphic specialization (e.g., to serpentine soil). While *S. medeirosii* and *S. juneae* are not restricted to specific substrates, they do exhibit an affinity to open, bare habitats. *Streptanthus medeirosii* occurs on steep slopes and roadside habitats that are prone to erosion. On the other hand, *S. juneae* occurs in openings in forest and chaparral habitats. As such, these two species fit well

TABLE 1. COMPARISON OF MORPHOLOGY OF PERENNIAL *STREPTANTHUS* IN SOUTHERN CALIFORNIA.

	<i>medeirosii</i>	<i>juneae</i>	<i>campestris</i>	<i>bernardinus</i>	<i>cordatus</i>
Petiole pubescence	glabrous	glabrous	often ciliate	glabrous	glabrous
Calyx shape	campanulate, inflated at base	tubular to narrowly campanulate	tubular to campanulate, not strongly inflated at base	campanulate, strongly inflated at base	tubular to campanulate, not strongly inflated at base
Sepal color	green to white to cream, rarely tinged pink at tip and on margins	green at base, tinged pink distally to universally pink light purple	green at base, tinged pink distally to dark maroon	greenish white to white to cream	green at base, tinged pink distally to universally pink to purple
Hairs at sepal tips	usually absent, sometimes present but sparse	absent	often present, numerous	usually absent	often present
Petal color	bases light green to yellow, distal quarter to half dark purple	bases light green to cream, tips maroon to dark purple	whitish green at base, tips dark purple	whitish green to cream, sometimes darker at tip, but not purple	whitish to green at base, and pink to maroon at least on apical half
Fruit shape	straight	arcuate	arcuate	erect	erect
Fruit width (mm)	2.4–4.1	1.6–3.2	2.0–3.5	2.5–6.0	2.0–3.5
Seed wing length at apex (mm)	0.4–1.3	0.1–0.5	0.06–0.3	0.1–0.4	0–0.3
Geographic range	Tehachapi Mountains	San Bernardino Mtns. south to Baja California, Mexico	San Bernardino Mtns. south to the Peninsular Ranges of San Diego Co.	Widespread in western U.S., absent from the Transverse and Peninsular Ranges of southern CA	MADROÑO

with the general ecology of *Streptanthus*, a genus that exhibits a remarkable number of rare, endemic species with a diverse array of specific habitat conditions.

Conservation Status

Locations of *S. medeirosii* are detailed in Fig. 3B. Currently, *S. medeirosii* is known only from three populations in the Tehachapi Mountains. The farthest east population (Jensen 524 and 2419; Location 1) is separated from the western-most population (*Laeger* s.n.; Location 3) by a linear distance of 15 km. The eastern-most population is the largest in areal extent and consists of approximately 100 plants growing over an area of approximately 0.2 ha. An intermediate population (Jensen 4764; Location 2) consists of approximately 50 plants over an area of 0.1 ha. The western-most population (Location 3) occurs within the Tejon Mountain Village development area and was not accessible during this study. Little is known about its population size or area of occupancy. Location 1 occurs on a slope above and below a major dirt road and is potentially threatened by road maintenance activities. Location 2 occurs in a remote, roadless area and has no known threats. Location 3 occurs close to an active cement mine within the boundary of a proposed residential development. The small total population size (150+ individuals) and area of occupancy easily makes *S. medeirosii* among the rarest of species in California, and it should be considered for conservation status ranking by the California Native Plant Society (CNPS), and for listing under the California and Federal Endangered Species Acts. Locations 1 and 2 occur within conserved areas on Tejon Ranch and are not imminently in danger of extirpation other than from road maintenance and stochastic events, but the status of Location 3 is unknown. Plants grow on steep eroded slopes in the Tehachapi Mountains and areas of suitable habitat have not yet been surveyed for new populations. Future fieldwork is likely to discover additional populations.

Locations of *S. juneae* are detailed in Fig. 3C. *Streptanthus juneae* is only known from five locations in the San Bernardino Mountains. Location 1 (Jensen 3784, 4773) contains more than 500 individuals. Location 2 (Jensen 4772) contains approximately 75 individuals. Location 3 (Hall s.n., Jensen 4774) contains fewer than 20 individuals. Location 4 (Munz 10577, Stoughton 582, Jensen 3785) contains approximately 50 individuals. Location 5 (Feudge 1107, Howe s.n.) was not visited and no population information is available. The California Natural Diversity Database (2017) lists an occurrence of *S. campestris* from Green Spot Campground, which is near existing locations of *S. juneae*. There is no specimen associated with this report and attempts to locate *Streptanthus* at this location in 2014 were unsuccessful. Reports of *S. campestris* at higher elevations of the San Jacinto Mountains were

evaluated as possible locations of *S. juneae*. Based on fieldwork and herbarium research these were determined to be *S. bernardinus*. *Streptanthus campestris* occurs in the southern foothills of the San Jacinto Mountains along Fobes Ranch Road (*Emmel* 1264, RSA821846) and the trail to Spitler Peak (*Emmel* 1413, RSA822990). Locations of *S. juneae* occur along roads or hiking trails and are thus potentially threatened by road maintenance, off-road vehicle impacts, and recreational activities. That said, these threats appear to be minimal at this point in time. Given its rarity, *S. juneae* should be considered for conservation status ranking by CNPS.

Another Related and Potentially-undescribed *Streptanthus* in the Santa Ynez Mountains

A perennial *Streptanthus* has been collected in the Santa Ynez Mountains along the Ocean View Trail by Burgess (1353; SBBG124166) in 1994 and Pollard (s.n.; SBBG39092, SBBG39091, CAS480337) in 1948. These collections have previously been identified as *S. campestris*. Their duration, height (<0.5 m tall), coriaceous leaves, lack of ciliate petioles on basal leaves, and lack of terminal flower clusters indicate that these plants are not *S. campestris*. The overall morphology of the Santa Ynez plants suggests a close relationship with the Southern California Clade. However, these collections lack floral material sufficient to determine them to species. Attempts to access the location of these collections were unsuccessful in 2015 and 2016. Efforts to extract high-molecular weight DNA from leaf tissue from *Burgess* 1353 were also unsuccessful. Future field work should focus on gaining access to the population of this *Streptanthus* in the Santa Ynez Mountains, so that it can be identified.

Notes on Morphological Characters used in this and Past Taxonomic Treatments

Al-Shehbaz (2005, 2012b) indicates that *Streptanthus bernardinus* and *S. campestris* are tetrady namous (two pairs of stamens with long filaments and one pair with short filaments), and that *S. oliganthus* and *S. cordatus* have stamens with three pairs of staminal filaments of three different lengths. Dissections of at least 22 flowers from individuals from multiple populations of each of these species conclusively indicate that all four of these taxa have stamens in three pairs of three different lengths. This was also observed in flowers at various stages of development from individual inflorescences from multiple populations of each species. In other words, *S. bernardinus* and *S. campestris* are conclusively not tetrady namous. Additionally, *S. juneae* and *S. medeirosii*, also have stamens of three different lengths. There are differences between species in the degree to which stamen lengths are unequal (e.g., the difference in stamen length between the longest and shortest pair is greatest in *S. cordatus*) and these differences may

be of taxonomic utility. Additionally, Al-Shehbaz (2012b) indicates that the proximal halves of petals are purple in *S. cordatus* and *S. oliganthus*, whereas proximal petal halves in *S. bernardinus* and *S. campestris* are white or pale yellow. Observations of fresh floral material indicate that the proximal halves of petals in *S. cordatus* and *S. oliganthus* are not consistently purple, and that this character should not be used in taxonomic keys.

These discrepancies serve to emphasize that floral characters in *Streptanthus* are best observed in fresh plant material, as colors, shapes and sizes in herbarium specimens can be obscured. Furthermore, even if sufficient floral material is available for dissection in herbarium specimens, the cumulative impact of destructive sampling specimens would adversely affect their preservation. The taxonomic key presented here is best used on plants in the field or on recently collected specimens that have not yet dried. This key makes use of fruit architecture and width to differentiate *S. oliganthus*, *S. cordatus*, and *S. medeirosii* from *S. longisiliquus*, *S. campestris*, *S. bernardinus*, and *S. juneae*. If fruits are absent from plants at collection time, emphasis should be placed on the collection locality to separate these groups of species. Additionally, collectors should note calyx shape, and the color of sepals and petals in the field, as changes in shape, size, and color occur during the drying process. Photographs of plants in the field can be helpful in making determinations.

CONCLUSION

The discovery of a new species on a sparsely explored portion of Tejon Ranch is not altogether unexpected. I found *S. medeirosii* during my floristic work on Tejon, and this discovery initiated research that became an important focus of my dissertation. My efforts to understand *S. medeirosii* in relation to other perennial *Streptanthus* led me to other mountain ranges in southern California. It was during these travels that I came to realize that plants, which had been called *S. campestris* in the San Bernardino Mountains did not, morphologically-speaking, match the species at its type location. These aforementioned plants are now described as *S. juneae*.

With few exceptions, research institutions have shunned floristic research as antiquated and based too much on observation (versus hypothesis testing). However, a few academic programs like Rancho Santa Ana Botanic Garden have continued to support and promote this research. It could be said that there are few better ways to formulate hypotheses than to get out and observe plants in the field. It was my floristic research that led me to discover *S. medeirosii* and this led me to study evolutionary patterns in perennial *Streptanthus* and the Thelypodiaeae, as a whole. These discoveries and my subsequent research give us insight into evolutionary trends in *Streptanthus* and the California flora. This research also adds two, new rare species to our

already-rich flora, clarifies how these species fit morphologically with other perennial *Streptanthus* and *Caulanthus*, and thus adds to our collective botanical knowledge. It is my hope that additional academic institutions will consider promoting floristic

research, not only because we need to know more about plant geography in an ever-changing world, but also because such research is a never-ending source of scientific inquiry.

KEY TO PERENNIAL *STREPTANTHUS* AND *CAULANTHUS* IN CALIFORNIA

1. Plants with unlobed basal leaves (often dentate); filaments in pairs at three different lengths (short, medium, long); plants generally glabrous (occasionally with trichomes on the tips of sepals and/or on the petioles of basal leaves)
 2. Inflorescences bracteate (plants biennial or short-lived perennial) *Streptanthus tortuosus*
 - 2'. Inflorescences ebracteate (plants perennial, sometimes short-lived)
 3. Cauline leaves petiolate *Streptanthus howellii*
 - 3'. Cauline leaves sessile, often amplexicaul
 4. Cauline and basal leaves of similar size, minimally reduced distally *Streptanthus barbatus*
 - 4'. Cauline and basal leaves dissimilar in size, reduced distally
 5. Fruit straight, ascending to erect, 2.6–6 mm wide; plants widespread in California and adjacent states, but not present in the Transverse and Peninsular Ranges of Southern California or the mountains of Baja California, Mexico
 6. Basal leaves entire, length of petiole often exceeding the length of the lamina, plants of Eastern California (Masonic Mountain, Sweetwater Mountains), and immediately adjacent areas in Nevada, and in the Wasuuuk Range, Nevada *Streptanthus oliganthus*
 - 6'. Basal leaves with at least some teeth along margins; length of petioles shorter than length of lamina; plants widespread or endemic to the Tehachapi Mountains
 7. Seed wings at tips of seeds almost always exceeding 0.5 mm long; calyx strongly campanulate; basal leaves with some teeth, but not strongly and deeply dentate; petioles not ciliate; sepals rarely with pink or purple pigmentation (if present, usually only in older flowers or on hyaline sepal margins); fruits with midvein sometimes visible but not prominent, margins not thickened; endemic to the Tehachapi Mountains. *Streptanthus medeirosii*
 - 7'. Seed wings at the tips of seeds less than 0.5 mm long; calyx not strongly campanulate, basal leaves usually deeply dentate, especially at apices; petioles ciliate or not; sepals with purple/red pigmentation, at least at tips; fruits with prominent midvein and thickened margins; widespread *Streptanthus cordatus*
 - 5'. Fruit arcuate, usually reflexed at maturity, usually not erect or ascending, 1.6–3.5 mm wide; plants of the Transverse or Peninsular Ranges or the mountains of Baja California, Mexico or the northern Sierra Nevada (*Streptanthus longisiliquus*)
 8. Plants of the northern Sierra Nevada *Streptanthus longisiliquus*
 - 8'. Plants of the Transverse or Peninsular Ranges of Southern California (and immediately adjacent areas) or of the mountains of Baja California, Mexico
 9. Sepals without purple or pink pigmentation; calyx campanulate, strongly inflated; petals without red or purple pigmentation *Streptanthus bernardinus*
 - 9'. Sepals with at least some purple or red pigmentation; calyx tubular to slightly campanulate, but not strongly inflated; petal tips red or dark purple
 10. Sepals uniformly dark purple; with a dense cluster of fertile flowers at apex of inflorescence; plants often taller than 1 m; leaves appearing thin, especially when dried; petioles of basal leaves often with ciliate margins; southeastern foothills of the San Bernardino Mountains south to Baja California, Mexico *Streptanthus campestris*
 - 10'. Sepals with some purple pigmentation, but not uniformly dark purple; dense cluster of fertile flowers at stem apex absent; plants usually less than 0.5 m tall; leaves appearing thick, coriaceous; basal leaf petioles without ciliate margins; endemic to the San Bernardino Mountains. *Streptanthus juneae*
 - 1'. Plants generally with pinnately lobed basal leaves; stamens tetradynamous (2 pairs with long filaments and 1 pair with short filaments); plants glabrous or hairy
 11. Stems strongly inflated *Caulanthus crassicaulis*
 - 11'. Stems not strongly inflated
 12. Basal leaves in rosettes; pedicels 1–6 mm long *Caulanthus major*
 - 12'. Basal leaves not in rosettes; pedicels 5–35 mm long *Caulanthus glaucus*

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NEW SPECIES AND A NEW VARIETY OF *NEMAACLADUS* (CAMPANULACEAE,
NEMAACLADOIDEAE) AND A KEY TO THE SPECIES

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ABSTRACT

In the course of preparing the treatment of *Nemacladus* (Campanulaceae, Nemacladoideae) for Volume 18 of *Flora of North America north of Mexico*, it has become apparent that several new taxa must be described and others recircumscribed. These are: two new species of uncertain affinities from the White Mountains and Inyo Mountains; in the *N. longiflorus* A.Gray group, a new species and a variety elevated to species; four new species in the *N. sigmoideus*/*N. secundiflorus* complex; and a new variety of *Nemacladus twisselmannii* J.T.Howell.

Key words: California, Campanulaceae, *Nemacladus*.

Nemacladus Nutt. is one of two genera in the Nemacladoideae M.H.G.Gustafsson (Campanulaceae Juss.), which is endemic to southwestern North America and central Mexico and most closely related to Cyphocarpoideae Miers, a Chilean endemic. Together these two subfamilies are sister to Lobelioidae Burnett, although the exact relationships are still unclear (Crowl et al. 2016). *Pseudonemacladus* McVaugh, the other genus in the subfamily, is monotypic and known only from the Sierra Madre Oriental in Mexico (Rzedowski 2019). *Pseudonemacladus* differs from *Nemacladus* in being perennial with a woody caudex, lacking a basal rosette, and having sub-opposite cauline leaves. In *Pseudonemacladus*, the flowers are not resupinate; in contrast to *Nemacladus* and all Lobelioidae, the filament tube and style bend away from the medial sepal before curling over. *Pseudonemacladus* lacks the conspicuous nectary glands and large cells attached to the filaments found in *Nemacladus*.

Nemacladus is annual, with a basal rosette, and few, if any, cauline leaves, which, when present, are alternate. *Nemacladus* flowers are resupinate or not, distinctly bilabiate or not, the petals distinct to base or connate proximally. Unlike Lobelioidae, the corolla lobes are not connate into lips, but the corolla may be 2-lipped, in which three lobes are opposite the other two, or 1-lipped, in which all five lobes are on one side, or nearly radially symmetric, with lobes evenly distributed. The ovary is partially inferior in all but the *N. longiflorus* A.Gray group, which have superior ovaries. The filaments are connate at least part of their length and recline or bend toward the medial sepal. The two filaments flanking the medial sepal bear conspicuous clusters of single, elongate cells sometimes attached to a multicellular pad. Most species have large nectar glands on the ovary apex. Pollen is presented on the

tip of the closed stigma lobes, which are exposed after the anthers flip back, compared with lateral hairs or papillae on the style in Campanuloideae (Shetler 1979), or pushed through the tube of connate anthers in Lobelioidae, or in a “pollen box” in Cyphioideae (Leins and Erbar 2003). The function of the large cells attached to the filaments is unknown. These cells reflect light, so they may mimic nectar, although the nectar glands appear to produce copious nectar as well. The cells may serve as heat repositories to warm pollinators, or they may perform a mechanical function in the movement of the filament tube/style. In summary, this is a very unusual genus within Campanulaceae.

Several factors make it difficult to identify *Nemacladus* in the field or in the herbarium. Small-flowered species tend to be self-compatible, self-pollinating, and may mature fruit even after being pressed (Morin unpublished data); specimens of these may only have capsules and senesced flowers even if collected in full bloom. Species of *Nemacladus* may grow intermixed or near each other, thus herbarium specimens are frequently mixed sheets composed of multiple species (Morin unpublished data). Since different species develop at different times, a collection may include immature plants of one species and mature plants of another. Most species of *Nemacladus* are very difficult to see in the field: the basal rosette is generally shriveled when in flower, the pedicels are so thin as to be nearly invisible, leaving only the flowers and fruits to be seen about 5 to 10 cm above the ground surface, which is often sand or fine gravel the color of the corollas.

Munz (1924) published the first comprehensive work on *Nemacladus*. He retained *Parishella* A.Gray as a separate genus and in *Nemacladus* recognized eight varieties grouped in three species (Table 1):

TABLE 1. COMPARISON OF PREVIOUS TAXONOMIC TREATMENTS OF *NEMACLADUS*.

Munz (1924)	McVaugh (1939)	Robbins (1958)	Morin (2008, 2012)
<i>Parishella californica</i> A. Gray	<i>Parishella californica</i>	n/a	<i>Nemacladus californicus</i> (A.Gray) Morin
<i>N. longiflorus</i> A. Gray	<i>N. longiflorus</i> var. <i>longiflorus</i> /var. <i>breviflorus</i> McVaugh	n/a	<i>N. longiflorus</i> var. <i>longiflorus</i> , var. <i>breviflorus</i>
	<i>N. glanduliferus</i> Jeps. var. <i>glanduliferus</i>	n/a	<i>N. glanduliferus</i>
	<i>N. glanduliferus</i> var. <i>orientalis</i> McVaugh	n/a	<i>N. orientalis</i> (McVaugh) Morin
	<i>N. ramosissimus</i>	n/a	<i>N. ramosissimus</i>
<i>N. ramosissimus</i> Nutt. var. <i>ramosissimus</i>			
<i>N. ramosissimus</i> var. <i>gracilis</i> (Eastw.) Munz	<i>N. gracilis</i> Eastw.	<i>N. gracilis</i> s.s.	<i>N. gracilis</i> s.s.
<i>N. ramosissimus</i> var. <i>pinnatifidus</i> (Greene) A. Gray	<i>N. pinnatifidus</i> Greene	n/a	<i>N. pinnatifidus</i>
<i>N. rigidus</i> Curran var. <i>rigidus</i>	<i>N. rigidus</i>	n/a	<i>N. rigidus</i>
<i>N. rigidus</i> var. <i>australis</i> Munz	<i>N. glanduliferus</i> var. <i>australis</i> (Munz) McVaugh	n/a	<i>N. australis</i> (Munz) Morin
<i>N. rigidus</i> var. <i>capillaris</i> (Greene) Munz	<i>N. capillaris</i> Greene	n/a	<i>N. capillaris</i>
<i>N. rigidus</i> var. <i>interior</i> Munz	<i>N. rubescens</i> var. <i>interior</i> (Munz) McVaugh	<i>N. interior</i> (Munz) Robbins	<i>N. interior</i>
<i>N. rigidus</i> var. <i>montanus</i> (Greene) Munz	<i>N. montanus</i> Greene	n/a	<i>N. montanus</i>
<i>N. rigidus</i> var. <i>rubescens</i> (Greene) Munz	<i>N. rubescens</i> Greene var. <i>rubescens</i>	n/a	<i>N. rubescens</i>
	<i>N. rubescens</i> var. <i>tenuis</i> McVaugh	n/a	<i>N. tenuis</i> (McVaugh) Morin var. <i>tenuis</i> /var. <i>aliformis</i> Morin
		<i>N. secundiflorus</i> Robbins	<i>N. secundiflorus</i> var. <i>secundiflorus</i> /var. <i>robbinsii</i> Morin
		<i>N. sigmoideus</i> Robbins	<i>N. sigmoideus</i>
			<i>N. twisselmannii</i> J.T.Howell
			<i>N. calcaratus</i> Morin

long-flowered *N. longiflorus*, campanulate-flowered *N. ramosissimus* Nutt., and petals distinct nearly to base in *N. rigidus* Curran. McVaugh (1939) published a revision of *Nemacladus*, and Robbins (1958) addressed issues in *N. gracilis* Eastw. Morin (2008, 2012) published the only recent treatments of the genus. Here we describe two new species from the White Mountains of uncertain affinity, a revision of the *N. longiflorus*, *N. secundiflorus* G.T.Robbins, and *N. sigmoideus* G.T.Robbins groups, and a new variety of *N. twisselmannii* J.T.Howell.

METHODS

Over the course of this study, more than 3500 herbarium specimens of *Nemacladus* from the herbaria listed in the Acknowledgments and more than 100 populations of *Nemacladus* in the field have been studied. Because so many characters are lost or difficult to see on herbarium specimens, a concerted effort to see as many populations of *Nemacladus* as

possible in the field began in 1993. Plants were photographed in the field and in the laboratory. Freshly collected plants were maintained in small vases until they could be photographed in the lab and pressed to best maintain characters. Flowers were preserved in formalin-acetic acid-alcohol (FAA) or 70% ethanol. Preserved whole flowers or with corollas removed were dehydrated, critical point dried, coated with gold-palladium, and viewed with the SEM to study the glands and staminal appendages. Samples for molecular sequencing were dried using silica. Study of morphological characters revealed consistent differences in architecture, leaf size and shape, bract shape and aspect, pedicel shape, flower orientation, sepal shape and aspect, corolla size, shape, and coloration, filament and anther coloration, and capsule shape. In most cases, these correlated well with geographical distribution and results of preliminary molecular analyses (Neff and Ayers unpublished data). Differences in flowering time, flower orientation, and corolla size and shape

can be expected to result in reproductive isolation between distinct species in *Nemacladus*. Supplemental Materials 1 lists images of holotypes included as Supplemental Figures.

Notes on Terminology and Measurements

On any flowering branch, generally there are one or two flower buds in the distal-most portion, one open flower below those, and developing capsules below that. Measurements of bract length, pedicel length, and internode length in the descriptions refer to the area just above and below an open flower. Angles of pedicels and of branches relative to the adjoining axis are approximate, to give an idea of openness or compactness of the plant. Abaxial or adaxial position of sepals and petals or corolla lobes refers to flowers as they appear when they open, whether they are resupinate or not. Therefore, in non-resupinate flowers there are two abaxial petals, whereas in resupinate flowers there are three abaxial petals. In non-resupinate flowers (Fig. 1A, B), the calyx consists of two paired adaxial sepals, two paired lateral sepals—called flanking sepals here, and a median unpaired abaxial sepal. For ovary and capsule dimensions, the percentage inferior approximates how much of the ovary is below the point at which the hypanthium ends. However, this changes as the capsule develops, with the ovary dome expanding above the hypanthium line, or the lower portion enlarging, or the distinction between hypanthium and ovary wall disappearing (as in *N. pinnatifidus* Greene), the sepals seeming to arise directly from the capsule wall.

TAXONOMIC TREATMENT

Two New Species from the White Mountains and Inyo Mountains of Uncertain Affinities

Populations from near the California/Nevada state border with sigmoid pedicels and small flowers usually have been identified as *Nemacladus sigmoideus*. Some of these plants proved to have a corolla similar to *N. orientalis* (McVaugh) Morin, sepals similar to *N. rigidus*, and pedicels similar to *N. sigmoideus* (Fig. 1A, B). A collection made in 1897 by Marcus E. Jones near Bishop, Owens Valley, California, may be the first collection of this taxon. Although often collected with *N. orientalis* or *N. sigmoideus*, or both, some collections of the new species by itself were also found. Photographs of this unusual form by Steven Matson (Fig. 1A, B) showed that the coloring of the corolla was also different from other species. We relocated two populations based on collections by James Morefield, making it possible to examine fresh material and preserve material for molecular analysis and SEM, from which we concluded this was an undescribed species.

***Nemacladus morefieldii* Morin & T.J.Ayers, sp. nov.**—Type: USA, California, Inyo County.

Near the SW base of Black Mountain, 1.8 mi, N4° of Wilkerson Springs, T8S R34E S33. Coarse mixed alluvium sloping 5°WSW with *Atriplex*, *Haplopappus*, *Psorothamnus*, *Menodora*, *Grayia*. Sporadically common annuals. Owens Valley drainage. Alt. 4350 feet. 06 May 1986. *James D. Morefield and Douglas H. McCarty* 3587 (Holotype: UC1545302!, Supplemental Fig. 1, Isotypes: ARIZ!, MO!, NY!, RSA!, RSA-POM!, UCR!).

Nemacladus morefieldii differs from other species of *Nemacladus* in having the combination of a sigmoid pedicel, nonresupinate flower, sepals different in size and shape, the two lateral sepals about 1/3 larger than the others, ovate, giving a winged appearance, the corolla bilabiate, with lobes distinct to base, adaxial 3 lobes white with maroon or orangey-brown shading on the margins (Fig. 1A, B.).

Plants erect, 4–14 cm tall, branched from base at 20–30°angles to the main stem, or 1.5–2 cm above base at about 70°, branches dichotomous in lower nodes, straight, angles narrow, secondary branches few or none. **Stems** brownish purple proximally, with short fine hairs proximally. **Leaves** rhombic to nearly round, 3–8 × 2–5 mm, ± fleshy, narrowed to broad base, margins entire, wavy, apex obtuse, surfaces with very fine, very short hairs adaxially, felty or granular abaxially. **Inflorescence** axis shallowly zig-zagged, internodes 5–8 mm long (progressively shorter distally); bracts appressed to and enfolding pedicel base, broadly ovate, 1–3 × 0.6–1.5 mm, ± fleshy, apex acute. **Pedicels** ascending at about 60° to axis, 8–15 (–22) mm long, about 0.2 mm diam., straight, becoming sigmoid and declining, abruptly upturned at tip. **Flowers** non-resupinate, held facing outward; hypanthium obconical, 0.5–1 mm tall, sepals fleshy, abaxial sepal deltate, adjacent sinuses wide, straight, adaxial 4 sepals unequal, the flanking 2 ovate, 1.2–1.5 × 0.4–0.8 mm, about 1/3 longer and wider than central 2, bowed, giving a winged appearance, central adaxial sepals lanceolate, 0.8–1.1 × 0.2–0.3 mm; corolla bilaterally symmetric, slightly cup-shaped at base, petals distinct to base, abaxial 2 lobes white, oblong-lanceolate, apex acute, tips appressed at anthesis, 1.2–1.6 mm long, adaxial 3 lobes white with maroon or orangey-brown shading on margins abaxially and adaxially, triangular, outer two bowed on outer margin giving a winged appearance; filaments connate in distal about 1/3, declined, white proximally, white or faintly maroon distally, (1–)1.5–1.8 mm long, transparent cells 4–6 per group, cylindrical, tip rounded, attached at base of filaments and at right angles to filaments, anthers white, about 0.2 mm long, pollen white; ovary 1/2–3/4 superior, stigma blue or rose-pink; nectaries flat, round in outline, yellow. **Capsules** about 4/5 superior, ± obconic, round in cross section, somewhat compressed horizontally, 1.5–2.6 × 1.5–2.4 mm, base rounded, apex rounded; sinuses flanking lower sepal not clearly differentiated from upper part of capsule,

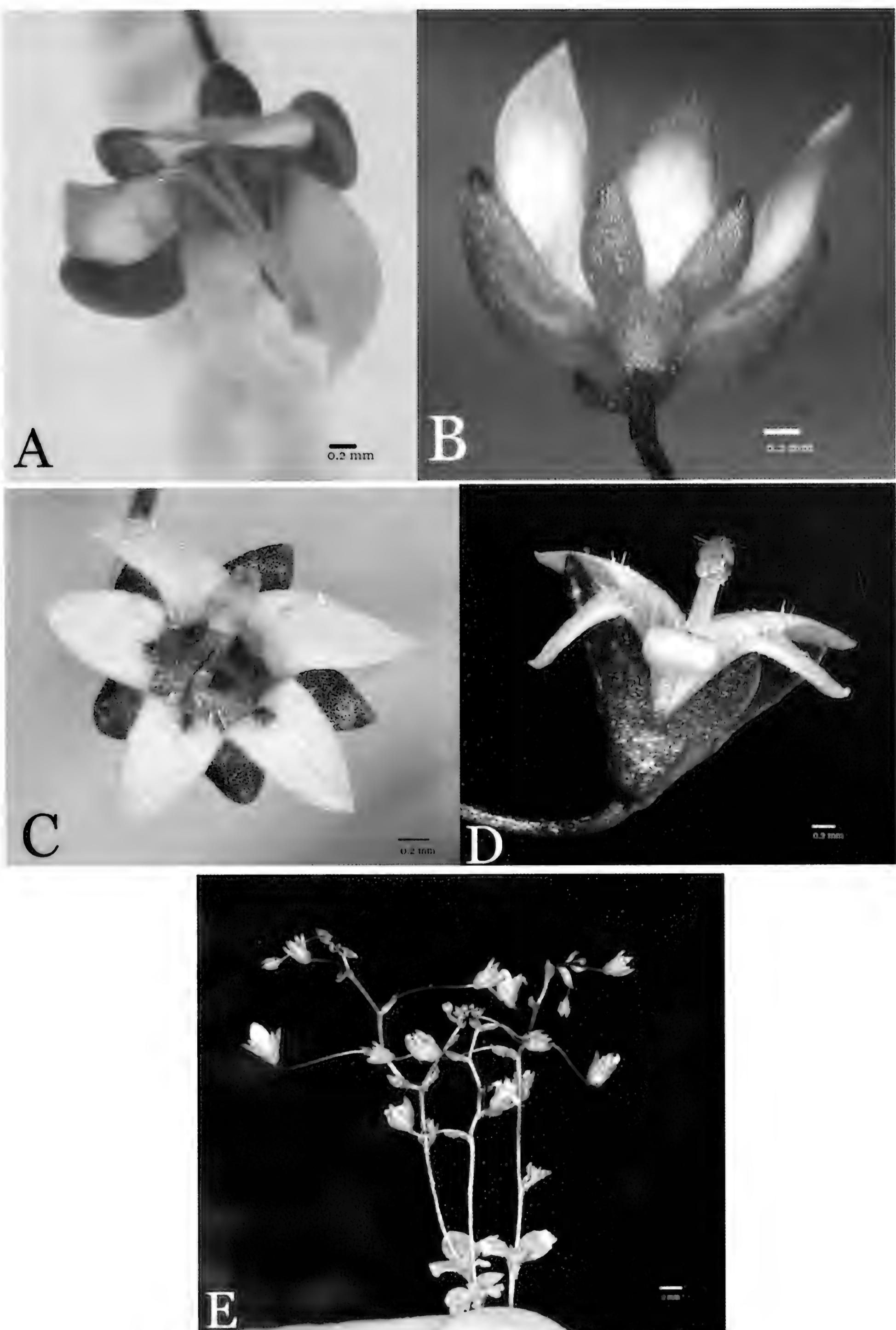


FIG. 1. *Nemacladus morefieldii* and *N. inyoensis*: *N. morefieldii*, A. flower front; B. flower back; *N. inyoensis*, C. flower front, D. flower side, E. entire plant. (photos: S. Matson).

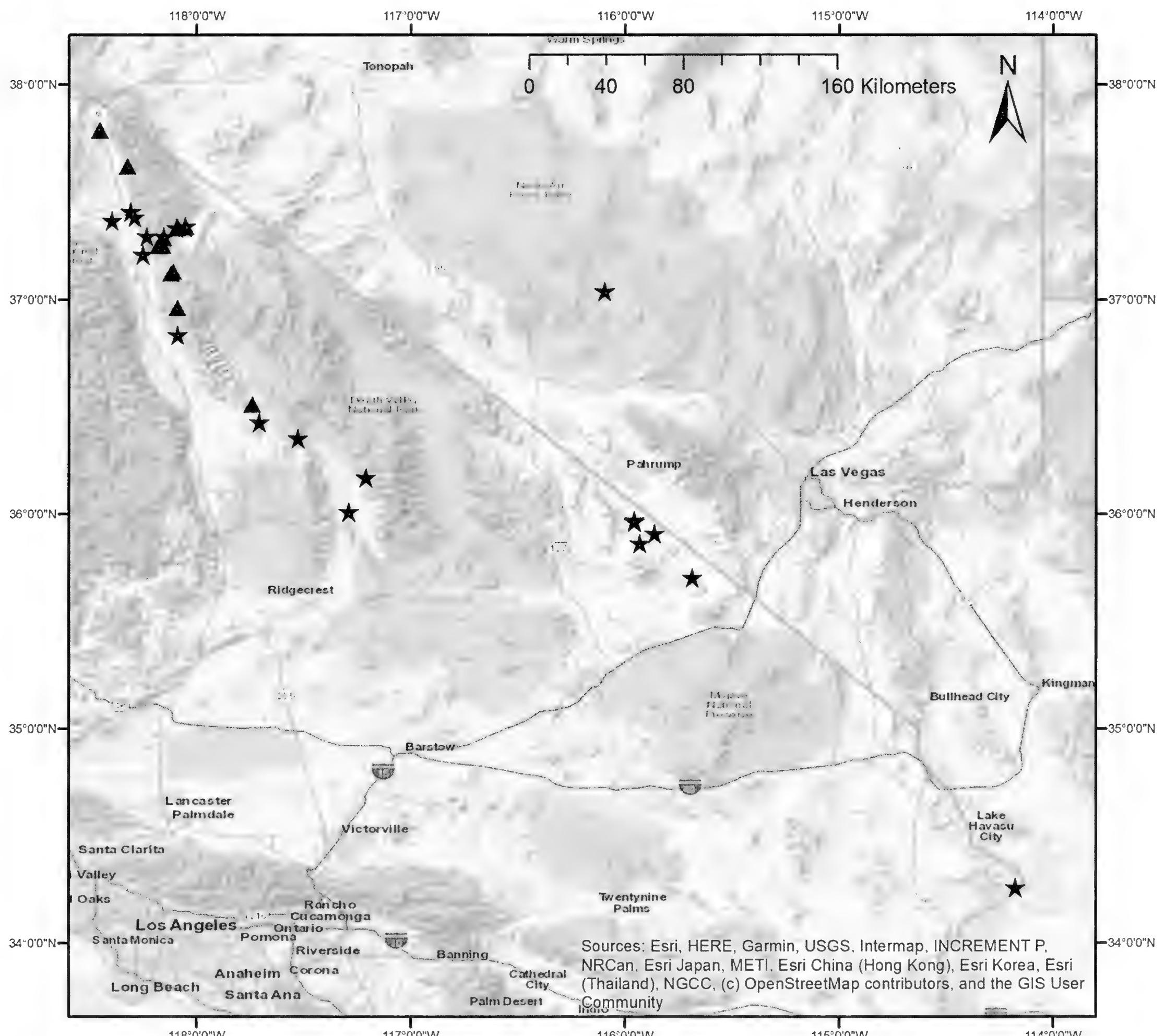


FIG. 2. Distribution of *Nemacladus morefieldii* (stars) and *N. inyoensis* (triangles).

abaxial sepal cocked downward, adaxial 4 sepals clasping in fruit. Seeds oblong, 0.5–0.6 mm long, surface reticulate.

Distribution and ecology. *Nemacladus morefieldii* occurs at 300–2200 m on volcanic and gravelly calcareous soil, shale talus, and in sandy, gravelly, desert washes, in the White and Inyo Mountains south along the California/Nevada state border to the Whipple Mountains (Fig. 2). Herbarium specimens of *N. morefieldii* usually have been identified as *N. sigmoideus*. Reports of *N. capillaris* from the eastern side of the Sierra Nevada are *N. morefieldii*.

Phenology. Flowering April through June.

Etymology. The species is named for Dr. James Morefield, Supervisory Botanist with the Nevada Natural Heritage Program, in recognition of his extensive work in the White Mountains of California and Nevada.

Representative specimens (localities abbreviated). USA. CALIFORNIA. Inyo Co.: Inyo Mountains, east of Independence, Mazourka Canyon, DeDecker 4059, 4060 (RSA 2 sheets, each with *N. sigmoideus*, *N. orientalis*, and *N. morefieldii*); Black Canyon, Duran 2730A; Cedar Flat, Duran 3290 (JEPS, UC); Bishop, Owens Valley, Jones s.n. (RSA-POM); between Jail and Hall Canyons, Panamint Valley, Kerr 452 (CAS); 5 mi NE of Darwin on old Death Valley Road, Kerr s.n. (CAS, RSA); 7.8 miles southwest of Deep Springs Maintenance Center, LeDoux, Dunn & Morris 807 (NY); Canyon to Santa Rosa Mine, 1.7 mi N38E of Poleta Mine, 3.3 mi ESE of Laws, Morefield 3400 (UC); Canyon to Santa Rosa Mine, south end of Inyo Mountains, Munz 11755 (CAS, NY, RSA WTU, (with *N. orientalis*)); Keanes Spring, Munz 12578 (MO, POM, UC); Slate Range, E of Trona, Peñalosa 2381 (CAS); NE Mojave Desert, southern Pahrump Valley, SW edge of Calvada Springs, 794 m, Sanders 39378b (UCR);

NE Mojave Desert, southern Pahrump Valley, WSW of Calvada Springs, 802 m, *Sanders & Onkar Singh* 39398 (UCR); west side of Pahrump Valley, *Wolf* 10593 (CAS, JEPS [JEPS sheet has *N. morefieldii* and *N. orientalis*], RSA, TEX, UC, WTU [UC and WTU sheets have *N. morefieldii*, *N. orientalis* and *N. sigmoideus*]). **Mono Co.**: East of Sierra Nevada: White Mtns, west base Piute Creek drainage c. 0.2 mi ne of powerhouse on Chalfant Loop Rd., 1319 m, *Howald* 4065 (UCR); North wall of Coldwater Canyon near its mouth, *Morefield* 3433 (ARIZ, GH, MICH, MO, NY, RSA, UC, UCR). **San Bernardino Co.**: 6.5 mi NNW of Horse Thief Springs, *Castagnoli et al.* 104 (CAS); Mesquite Mountains ca. 1.5 air miles northeast of Winters Pass, 1213 m, *Bell* 2624 (RSA, with *N. orientalis*); Sonoran (Colorado) Desert, Whipple Mountains, Dune OHV area near Echo Point/Echo Lodge, *DeGroot et al.* 2733 (with *N. orientalis*) (ARIZ, CAS, RSA, UCR). USA, NEVADA. **Clark Co.**: Las Vegas, on the mesas, *Goodding* 2319 (MO, NY). **Nye Co.**: Nevada Test Site, *Beatley* 3605 (DS [with *N. orientalis*], RENO).

Steve Matson discovered, photographed, and collected an unusual *Nemacladus* in the Inyo Mountains in 2010. The collection was of just a few small plants, not enough to determine whether it was an odd *N. sigmoideus* or a new species. Most notable in the photographs were dark maroon lines on the midveins of the three abaxial corolla lobes of the small, cup-shaped corolla. Three large populations were found by Matson, A. Schusteff, and M. Purdy in May and June, 2019, providing enough material to confirm this as an undescribed species that shares with *Nemacladus rigidus* dark stem, leaves, bracts, hypanthium, sepals, and mature capsule, and broadly deltate sepals; with the new species with small cup-shaped corolla described later in this paper, it shares a shallowly cup-shaped corolla, the three abaxial lobes oblong-lanceolate and the two adaxial lobes divergent (Fig. 1C, D, E).

Nemacladus inyoensis Morin & T.J.Ayers, sp. nov.—

Type: USA, California, Inyo County; Inyo Mountains, Harkless Flat Road, Forest road 9S13, 37.1167, -118.1158. Rocky limestone soils in sparse pinyon juniper woodland. 22 May 2019. *Matson* 2820, with *Aaron Schusteff* and *Martin Purdy*. Holotype: UC!; isotype ASC!

Nemacladus inyoensis differs from other *Nemacladus* species in its combination of bracts, hypanthium, and sepals having a very dark purplish-green color, corolla being cup-shaped, white to cream-colored with maroon stripe from throat to base on abaxial 3 lobes, and small, 2.1–2.4 mm; transparent cells being thin, cylindrical, attached to oblique appendage on filaments; and capsule dark brownish greenish purple, large, base flat to obtuse.

Plants erect, height above rosette 2–10 cm, (in some plants the rosette is 14–20 mm above the root/stem interface), reddish brown, branches few, from

base and upper nodes, at about a 45° angle from main axis, first branch 1–2.5 cm above rosette. **Stems** dark reddish brown, glabrous. **Leaves** elliptic to ovate, 1–4 × 0.5–3 mm, base cordate to obtuse, margins entire, apex acute to obtuse, surfaces glabrous or with sparse or dense broad or slender white hairs abaxially and adaxially. **Inflorescence** axis shallowly zigzagged, internodes 2–4 mm; bracts straight, aligned with pedicel, green with reddish margin, broadly ovate, 1–1.5 mm long, base cupped under but not enfolding pedicel base. **Pedicels** at 90° to axis, 5–12 mm long, 0.1 mm diam., shallowly curved, in fruit nearly straight. **Flowers** resupinate, bilaterally symmetric, hypanthium dark purplish green, obconic, 1.1–1.5 mm long, sepals erect, dark purplish green, broadly deltate, 1–1.5 mm long, flanking sepals longer than abaxial sepals, somewhat fleshy, base slightly narrowed, apex acute, apiculate, surface with clear, crystalline raised areas; corolla bilaterally symmetric, total length 2.1–2.4 mm, petals connate about 1/2 proximally to form a shallow cup, abaxial 3 lobes white to cream colored with deep maroon line on central vein from throat to base, oblong-lanceolate, adaxial lobes divergent, white to cream-colored, lower margin somewhat curved, upper margin straight; filaments connate in distal 1/2–1/3, arched over, grayish white to pale blue, apex glabrous or with few long hairs, transparent cells 6–8 per group, attached to broad, hockey-stick shaped pad on filaments, very slender, cylindrical, blunt-tipped, anthers pale blue, about 0.3 mm long; ovary about 9/10 inferior, nectaries yellow. **Capsules** 3/10–1/2 inferior, dark purplish green, base obtuse to flat, apex rounded to acute, 2.5–3 × 2–3 mm, sepals longer than valves, erect in fruit. **Seeds** oblong, 0.8–0.9 mm long, surface of rows of shallow pits separated by low ridges.

Distribution and ecology. *Nemacladus inyoensis* occurs in limestone, sandstone, and granite rubble and granite washes in pinyon juniper woodland and upper desert shrubland, at 1680–2600 m in the Inyo and White Mountains (Fig. 2).

Phenology. Flowering May–June.

Etymology. *Nemacladus inyoensis* was first discovered in the Inyo Mountains, Inyo County, California. The species name reflects its original discovery in the Inyo Mountains of eastern California.

Paratypes. USA. CALIFORNIA. **Inyo Co.**: Inyo Mountains, Ridge just south of Badger Flat, open pinyon juniper forest with *Penstemon*. 36.958, -118.0878. 2636 m. 20 June 2010. *Matson* 2539 (UC). White Mountains, side canyon running north from Westgard Pass road (CA Hwy 168) about 1 mi. ENE of Batchelder Spring and about 1 mile WSW of the narrows. Owens Valley drainage. Locally abundant. Gravelly calcareous alluvium in dry open wash along bottom of canyon draining southward, with *Eriogonum nidularium* Coville, *Diplacus parryi* (A.Gray) G.L.Nesom & N.S.Fraga, *Eriogonum*

TABLE 2. COMPARISON OF MORPHOLOGICAL FEATURES OF *NEMACLADUS BREVIFLORUS*, *N. LONGIFLORUS*, AND *N. RICHARDSSIAE*.

	<i>Nemacladus breviflorus</i>	<i>Nemacladus longiflorus</i>	<i>Nemacladus richardsiae</i>
Height	1–7 cm	(2.5)–7–21 cm	5–15 cm
Basal leaves	1.5–4 mm long	3–12 mm long	1.5–7 mm long
Internodes	2–5 mm long	3.5–7 mm long	4–7 mm long
Bracts	ascending, lanceolate	appressed to pedicel, elliptic to ovate	appressed to and enfolding pedicel base, linear- lanceolate
Pedicels	5–8 mm long	6–25 mm long	10–20 mm long
Sepals	linear lanceolate	elliptic	lanceolate
Corolla tube shape, lobes aspect	cylindrical, lobes rotate	cylindrical, lobes rotate	infundibuliform, lobes spreading
Corolla tube length	1.5–3 mm long, 1–1.5 times as long as sepals	5–8 mm long, 4–8 times as long as sepals	2.5–3 mm long, 2 times as long as sepals
Capsule	urceolate, 2–3 mm tall	fusiform, 3–5 mm tall	oblong-ovoid, 3–3.5 mm tall

fasciculatum Benth. var. *polifolium* (Benth.) Torr. & A. Gray, *Stipa speciosa* Trin. & Rupr., *Phlox stansburyi* (Torr.) A. Heller, *Lupinus flavoculatus* A. Heller, *Eriogonum inflatum* Torr. & Frém., etc. Corollas white to cream colored, 3 lobes medially maroon streaked near base. 6470 ft (1972 m), 37.24931° N, –118.17576° W ± 10 m. 9 June 2019. James D. Morefield 5896 (UC). Westgard Pass, Cedar Flat just east of White Mountain Road about 0.4 miles northwest of its intersection with California Hwy 168. Owens Valley drainage. Abundant on the flats. Level calcareous gravel and silty soil among shrubs, with *Pinus monophylla* Torr. & Frém., *Juniperus osteosperma* (Torr.) Little, *Artemisia nova* A. Nelson, *Artemisia tridentata* Nutt., *Oreocarya hoffmannii* (I.M. Johnst.) Abrams, *Cordylanthus kingii* S. Watson ssp. *helleri* (Ferris) T.I. Chuang & Heckard, *Cryptantha gracilis* Osterh., *Phlox stansburyi*, *Eriastrum wilcoxii* (A. Nelson) H. Mason, *Lupinus brevicaulis* S. Watson, etc. Corollas white to cream colored, 3 lobes medially maroon streaked near base. 7350 ft (2240 m), 37.28540°N, –118.15690°W. 23 June 2019. James D. Morefield with Steve Matson, Martin Purdy 5902 (UC). **Mono Co.:** White Mountains, north side of Jeffrey Mine Canyon near bottom, 0.1 miles WSW of Jeffrey Mine map marker, Hammil Valley-Owens Valley drainage. Light colored metamorphic scree and colluvium in bed of foot trail sloping 5° south near bottom of steep canyon, with *Pinus jeffreyi* Grev. & Balf., *Pinus monophylla*, *Artemisia tridentata*, *Artemisia nova*, *Chamaebatiaria millefolium* (Torr.) Maxim., *Eriogonum rupinum* Reveal, *Diplacus parryi*, *Festuca octoflora* Walter, etc. Corollas white to cream colored, 3 lobes medially maroon streaked near base. 7105 ft (2166 m), 37.61858°N, –118.32289°W (±5m). 22 June 2019. Morefield 5897, with Matson and Purdy. See also online images (Supplemental Materials 2).

Nemacladus longiflorus Complex

Nemacladus longiflorus is conspicuous with its resupinate flowers, long, bilabiate corollas, (Fig. 3D) and superior ovary and capsule. It was the second

species named in the genus, by Asa Gray (1877). Var. *breviflorus* was added by McVaugh in 1939 based on its shorter corolla, much shorter filament tube, smaller stature, and more pubescence. *Nemacladus breviflorus* is smaller than *N. longiflorus* and has a corolla tube about equal to slightly longer than the sepals, versus 4–8 times the length of the sepals in *N. longiflorus*. *Nemacladus breviflorus* often has a compact, curly look, with a zigzagged axis (vs. nearly straight axis in *N. longiflorus*), much shorter internodes, short, very curved pedicels, and small, very hairy basal leaves (Table 2, Figs. 3A, B.). The difference in corolla length alone would be a barrier to cross-pollination, and although the two taxa occur in close proximity to each other in some localities, *N. breviflorus* is more common in Transverse Ranges and San Jacinto Mountains, whereas *N. longiflorus* is more common in the Laguna, Palomar, Cuyamaca, Volcan, and San Jacinto mountains and Anza Borrego desert. Plants somewhat intermediate between these two taxa are rare, but have been reported from Whitewater Canyon, Riverside County.

Nemacladus longiflorus occurs in chaparral, oak woodland, and mixed conifer forests, in sandy washes and burned areas at 100–2200 m. It is found in the San Bernardino, San Gabriel, South Coast, and Peninsular Ranges, south to Sierra San Pedro Martír in Baja California (Fig. 4). A collection by Clokey (6928), north of Barstow, well out of the range of *N. longiflorus*, contains a few plants of *N. longiflorus* with mostly *N. rubescens*.

***Nemacladus breviflorus* (McVaugh) Morin & T.J.Ayers, comb. nov.** *Nemacladus longiflorus* A. Gray var. *breviflorus* McVaugh, Amer. Midl. Naturalist 22: 526. 1939.—Type: USA, Arizona, Pima County, near Roadside Mine on the Tucson Ajo Highway. Mar. 27, 1927. Peebles et al. 3754 (holotype: US1367475!; isotypes ARIZ!, RSA!).

Plants erect, 1–7 cm tall; branches many from base, narrow, at 25° angle to main stem, secondary branches few, at 70–90°. **Stems** reddish brown,

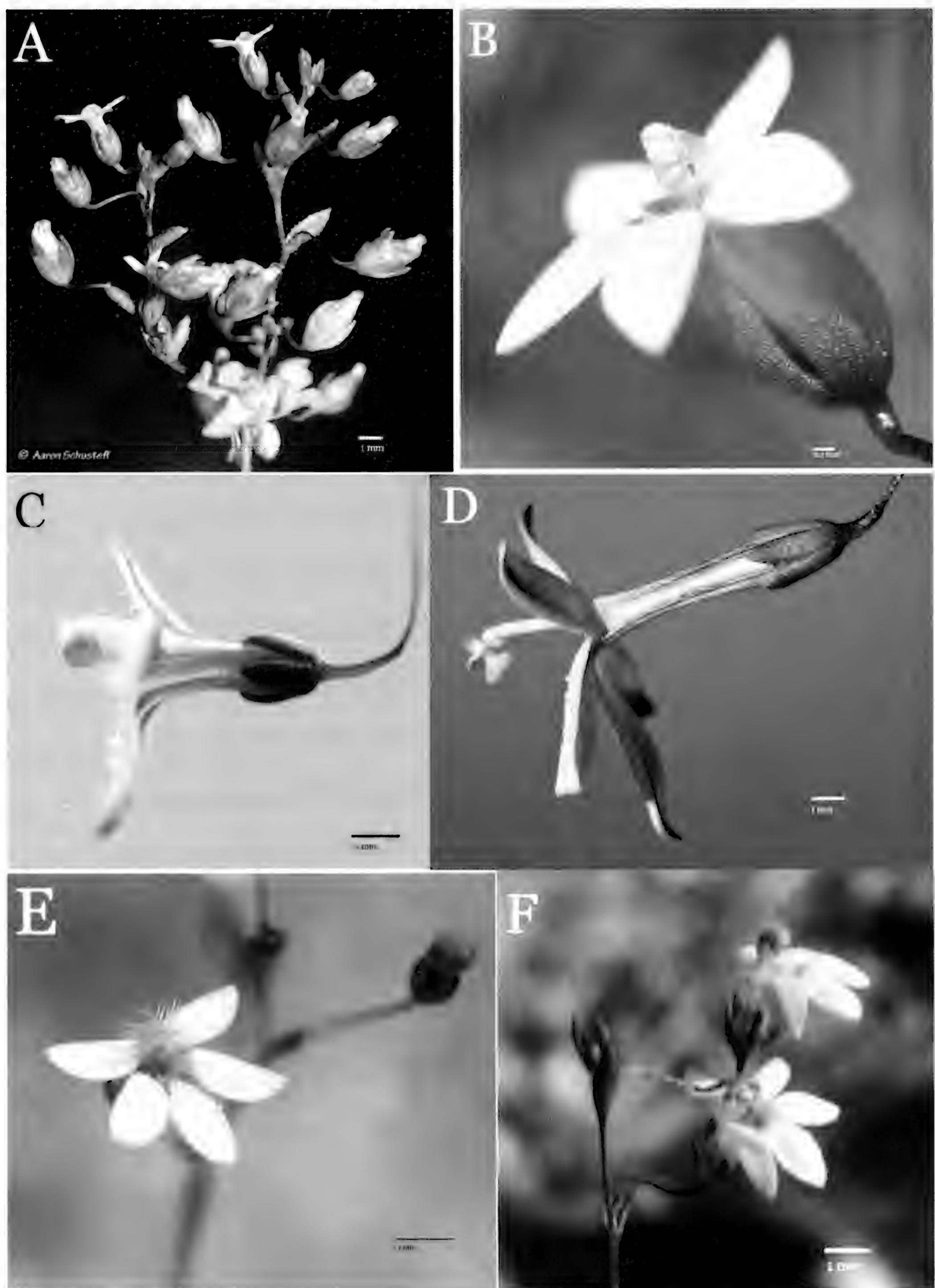


FIG. 3. *Nemacladus* flower comparisons: *Nemacladus breviflorus* A. habit., photo by A. Schusteff. B. flower, photo by N. Morin; *Nemacladus richardsiae*, C. flower, photo by N. Morin; *Nemacladus longiflorus*, D. flower, photo by Jon Rebman. *Nemacladus bellus*, E. flowers, photo by N. Morin; *Nemacladus secundiflorus* var. *secundiflorus*, F. flowers, photo by N. Morin.

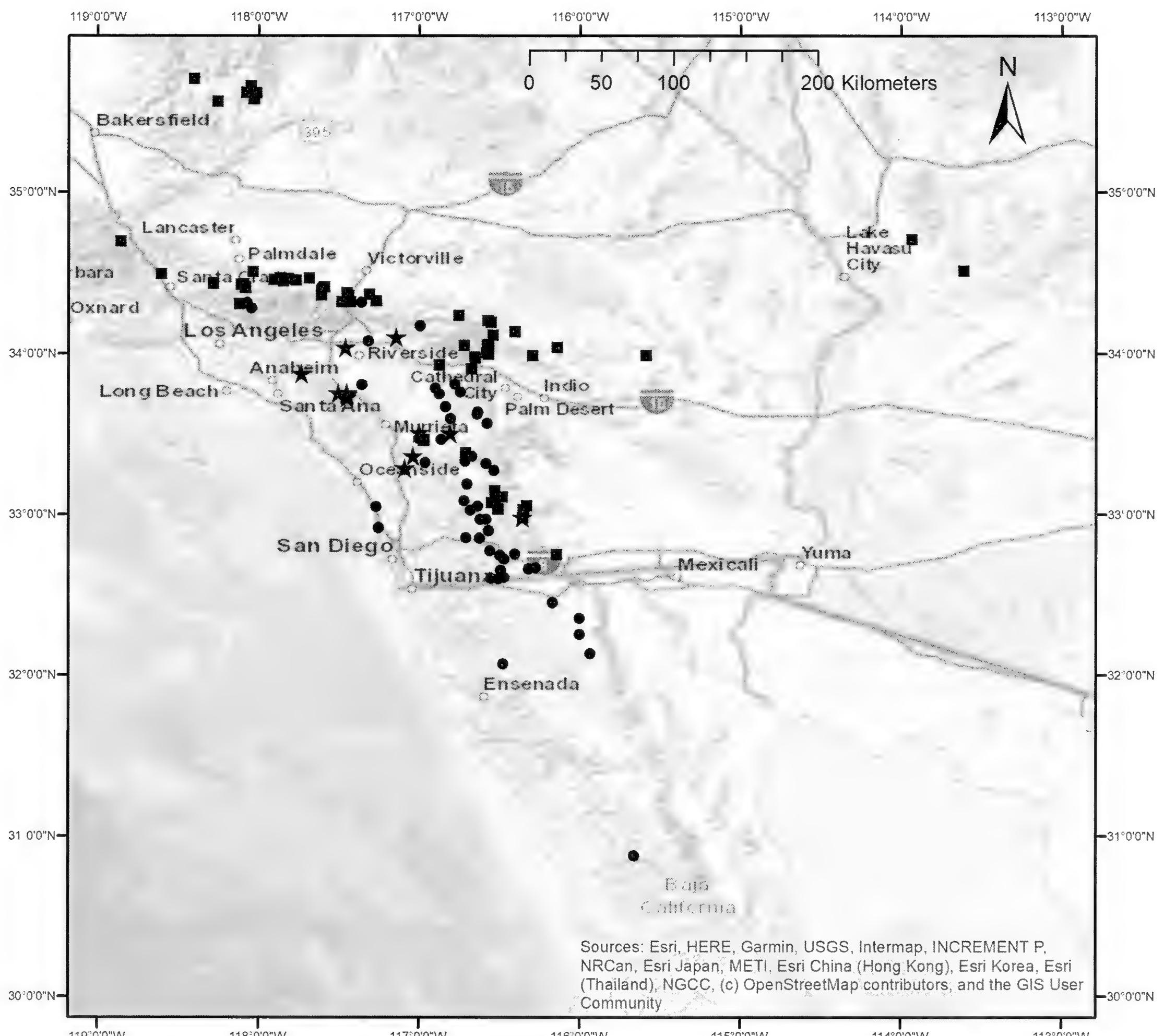


FIG. 4. Distribution of *Nemacladus richardsiae* (stars), *N. longiflorus* (circles), and *N. breviflorus* (squares). The locations of the *N. breviflorus* populations in Arizona and Utah are not shown.

glabrous or densely hairy. **Leaves** oblanceolate to ovate or oblong, 1.5–4 × 1–3 mm, base tapered or abruptly narrowed to a winged petiole, margins entire to finely crenate, apex broadly acute to obtuse, surfaces usually densely hairy, sometimes nearly glabrous. **Inflorescence** axis strongly zigzagged, internodes 2–5 mm long, bracts ascending, lanceolate to broadly lanceolate, 2–3 mm long, apex acute. **Pedicels** widely spreading, 70–90° to axis, often declined below its node, 5–8 mm long, about 0.1 mm diam., deeply sigmoid, proximally forming an ascending arch, distally deeply curved, tip abruptly curved. **Flowers** resupinate; hypanthium 0, sepals all alike, erect, appressed to corolla, linear lanceolate, 1.5–2 mm long; corolla salverform, bilaterally symmetrical, conspicuously 2-lipped, divided 1/2 or less to base, tube white with maroon lines abaxially, cylindric, 1.5–3 mm long, 1–1.5 times as long as sepals, abaxial lobes 3, spreading, white with yellow

spot on base, 3–3.5 mm long, central lobe elliptic, acute, 2 flanking lobes oblique-elliptic, about 4/5 length of central lobe, acute, adaxial surface with short, erect, white papillae, adaxial lobes 2, erect to slightly spreading, elliptic, acute, surface with short, erect, white papillae; filaments straight, connate in about distal 1/2, extended just beyond corolla tube, white, 2–3 mm long, tip abruptly curved down, hairs very short, transparent cells attached about 2/3 from base, slender, acute, 0.05–0.1 mm, anthers white or grayish, 0.25–0.3 mm long; ovary superior, oblong-ovoid, nectaries green, low mounds on side of ovary. **Capsule** superior, urceolate, 2–3 mm tall, base rounded, narrowed distally, rounded at tip, valves entire. **Seeds** ± round, 0.4 mm long, surface with rows of large pits.

Distribution and ecology. *Nemacladus breviflorus* occurs on sandy or gravelly slopes and in washes, in juniper woodland, sagebrush scrub, Joshua tree

woodland, and gray pine-oak woodland, at 300–1400 m. in the Transverse and Peninsular ranges and westernmost Mojave Desert, south to northern Baja California; disjunct populations occur in the Kern River and Cyrus canyons, Kern County (Fig. 4). Collections from the Colorado Plateau in Utah (e.g. Fertig 21062) are highly disjunct and occur in sandy openings and in undisturbed biological soil crust areas and orangish-red deep stabilized sand dunes. The Arizona collections, from Mohave County, are also disjunct. The type locality, in Pima County, Arizona (T. H. Kearney; R. H. Peebles & G. J. Harrison, 3754), is the only collection from that area. This species is found near, and sometimes mixed with, *N. longiflorus* in California.

Phenology. Flowering March–June (July).

In 2010, Thomas Chester alerted the senior author to a population of *Nemacladus longiflorus* in the Temescal Canyon. Although the plants generally resemble *Nemacladus longiflorus*, the funnelform shape of the corollas is unlike any other species in the genus, so significantly that recognition as a separate species is warranted. Lee Lake, in Indian Wash, Temescal Canyon, the type locality for the new species, has been a common botanical collecting spot at least since the early 1900s, and collections of *Nemacladus* from here date back to 1922.

***Nemacladus richardsiae* Morin & T.J.Ayers, sp. nov.**
TYPE: USA, California, Riverside County. Temescal. Sandy Wash. April 28, 1922. Munz 5024 (Holotype: UC 219192!, Supplemental Fig. 2; isotypes CAS!, DS!, MO!, POM!, RSA!, UC!).

Nemacladus richardsiae differs from other *Nemacladus* in having the combination of a large, 5–6.3 mm, infundibuliform corolla, the tube gradually widening and the lobes spreading from the same plane as the tube, and a superior ovary (Fig. 3C).

Plants erect, 5–15 cm tall; branching 1.5–5 cm above base, at 60–80° to main stem, rarely branching from base, secondary branches few, at 40–50°. **Stems** reddish brown, glabrous. **Leaves** lanceolate to ovate, obovate, or rhomboid, 1–7 × 0.5–3 mm, base tapered, margins shallowly crenate or with a few sharp teeth, apex obtuse to sharply pointed, surface glabrous or densely hairy, hairs short, white, appressed, some of them curly. **Inflorescence** axis nearly straight, internodes 4–7 mm long; bract bases appressed and enfolding pedicel base, straight, or proximal ones bent back at middle, otherwise erect and aligned with axis or aligned with pedicel base, lanceolate to linear-lanceolate, 1.5–3 × 0.6 mm, apex attenuate. **Pedicels** at 70–90° to axis, 10–20 mm long, about 0.1 mm diam., sigmoid, proximal curve broad, distal curve abrupt, tip abruptly curved. **Flowers** resupinate; hypanthium 0, sepals all alike, erect, lanceolate, 1.4–1.5 (–4) × 0.4–0.5 mm, narrowed at base; corolla infundibuliform, bilaterally symmetric, conspicuously 2-lipped, total length 5–6.3 mm,

divided 1/2–3/5 to base, pale pink, or cream-colored with broad pink stripes on tube and maroon splotches on lobes abaxially, a yellow spot on base of each abaxial lobe, adaxially hairy and papillate; tube flared, 2.5–3 mm long, about twice the length of the sepals, lobes extend from tube, not abruptly rotate, central abaxial lobe elongated obovate, about 3 mm long, about 1/4 longer than flanking lobes, obtuse, flanking lobes obovate, obtuse, about 2.5 mm long, 2 adaxial lobes ovate, acute, about 2 mm long; filaments slightly arched, extended well beyond corolla tube, connate in about distal 1/2, pale lavender blue, tube 2–4 mm long, tip curved down, apex densely short-papillate, appendages attached about 2/3 from base, cells slender, acute, 0.15 mm long; anthers pale lavender blue, 0.3–0.5 mm long, pollen cream-colored; ovary superior, oblong-fusiform, nectaries green, low mounds on side of ovary. **Capsule** superior, oblong-ovoid, 3–3.5 × 1.5–2.2 mm, base rounded, apex blunt, opening by two valves, the valves entire. **Seeds** nearly round, 0.4 mm long, surface with rows of large pits.

Distribution and ecology. *Nemacladus richardsiae* occurs on sandy flats of alluvial fans, in creosote scrub at 300–500 m, in Temescal Canyon, Riverside County south to San Luis Rey, San Diego County (Fig. 4), with an outlying population northeast of San Bernardino collected by Parish in 1888, supported by an image in iNaturalist taken in 2019 (Echols 2019) from just north of Mentone, San Bernardino County. In a good year, with many plants blooming, the pink color of the corollas makes a kind of pink haze over the ground.

Phenology. Flowering March through June.

Etymology. The species is named for Dr. Jennifer H. Richards, professor of Biology at Florida International University, who has studied the plants in the field with the senior author while accompanying her on many *Nemacladus* collecting trips. Dr. Richards's insight into the floral morphology of the genus has been invaluable.

Representative specimens. USA. CALIFORNIA. **Riverside Co.:** Lee Lake, Baer s.n. 1923 (POM); Temescal Canyon: east side of Indian Wash between I-15 and Temescal Canyon Road, Boyd 1700 (ARIZ, HSC, NY, RSA, TEX, UCR); Temescal Canyon: Alluvial benches of Indian wash just south of Interstate 15, Boyd 1753 (ARIZ, NY, RSA, TEX, UCR); Wilder's near Riverside, Brandegee s.n., 1905, (POM, UC); 9 mi W of Anza, Campbell 16133 (RSA); Temecula River, Jepson 1555A (JEPS); Cleveland Forest, Maxfield 51 (CAS); Temescal Canyon: east side of Indian Wash between I-15 and Temescal Canyon Road, Morin & Richards 657 (UC); Temescal Canyon, Peirson 2920 (CAS, DS, RSA); Temescal Valley: Indian Wash, SW of I-15, S. side of De Palma Rd., 700–1100 ft WNW of intersection with Glen Eden Rd., Provance 417-68 (UCR); Temescal Mts., Reed 5140 (POM); Eastern foot of Santa Ana Mtns., Temescal Canyon near Lee

(Corona) Lake, 0.1 mi. SW of the dam, south of Temescal Canyon Rd., Sanders 41530 (UCR). **San Diego Co.:** Wilderness Gardens, Scott s.n., 1983 (SD); Pala: alluvial fan of Magee Creek, southern foothills of the Agua Tibia Mtns. and adjacent San Luis Rey River Valley, White & DeVries 7328 (RSA). See also online images (Supplemental Materials 2).

The *Nemacladus sigmoideus* Complex

More difficult to study and less well understood than the showier species of *Nemacladus* are the ones with small white corollas. *Nemacladus ramosissimus*, which has cup-shaped corollas, was the first species described in the genus, and initially all small-flowered species were placed here. *Nemacladus ramosissimus* is easily recognized by its straight axis and erect, linear to oblong-lanceolate bracts. Munz (1924) included *N. gracilis* and *N. pinnatifidus* in *N. ramosissimus* as varieties; McVaugh (1939) recognized them as species, but maintained Munz's general concept of *N. gracilis*, which is to say everything with a sigmoid pedicel and small white flower not *N. pinnatifidus* or *N. ramosissimus* was included in *N. gracilis*.

Robbins (1958) determined that *N. gracilis* should be split into three species: *N. gracilis*, *N. secundiflorus* G.T.Robbins, and *N. sigmoideus* G.T.Robbins. *Nemacladus gracilis*, as Robbins circumscribed it, is limited to the Inner South Coast Range from Merced County south to Kern County, and in the foothills of the Tehachapi Mountains (Fig. 9). It has short internodes, short, very thin pedicels, and corolla tube base wider than the hypanthium.

Robbins (1958) included in *N. secundiflorus* plants with a "relatively long corolla-tube which often noticeably surpasses the calyx (for about a distance of 1 mm or slightly more); its wide-spreading upper corolla-lobes; its relatively stout pedicels that commonly spread at right angles to the branches (although in older plants they may display more or less of a sigmoid curve); its often strongly secund racemes, and its huge anthers." These plants were from the South Coast Range. He noted two exceptions to this general description: plants with small corollas from San Benito County, now recognized as *N. secundiflorus* var. *robbinsii* Morin, and plants from the Greenhorn Mountains in Kern County that "show considerable variation in the degree of pedicel arching, and secund racemes are evident only on an occasional branch." The Greenhorn Mountain populations are recognized here as a distinct species. In addition to characters mentioned by Robbins, they differ from *N. secundiflorus* var. *secundiflorus* (Fig. 3F) and var. *robbinsii* in having basal leaves broadly elliptic to ovate-deltate, 1.2–4 mm long, with margins shallowly toothed or wavy. *Nemacladus secundiflorus* basal leaves are oblanceolate to spatulate, 1.5–12 mm long, the margins irregularly lobed.

***Nemacladus bellus* Morin & T.J.Ayers, sp. nov.—Type:**
USA. California. Kern Co., dominant associated

species: *Quercus wislizeni* var. *frutescens* Engelm., *Cercocarpus montanus* [probably *Cercocarpus betuloides* Nutt. var. *betuloides*]. Upper reaches of the *Pinus sabiniana* D.Don belt on southwesterly facing slope, in loose granite gravel along road over Greenhorn Mountain (on the eastern side of the mountain) exactly 5 miles above junction of this road with road to Kernville; elevation 4,000 ft. June 1, 1954. *Bacigalupi and Robbins* 4538 (Holotype JEPS5490!, Supplemental Fig. 3). Additional note by G. Thomas Robbins on the specimen, 16 Feb. 1956: "Provisionally assigned to *N. secundiflorus* G.T.Robbins ined. on the basis of the rather large corollas and the outline of the basal leaves. Racemes are not secund, however, and the pedicels are somewhat more variable in curvature than in *N. secundiflorus*."

Nemacladus bellus differs from other species of *Nemacladus* in having the combination of basal leaves broadly elliptic to ovate-deltate, margins shallowly toothed or wavy, not irregularly lobed; inflorescence zigzagged, internodes 2–5 mm long, flowers not (or very rarely) secund (Fig. 3E); corolla with cylindrical tube 2–2.5 mm long, lobes 2–2.5 mm long; filaments and anthers white or pale lavender, the anthers about 0.4 mm long, transparent cells on filaments narrow, attenuate; capsule about 1/4 inferior, round, sepals erect in fruit.

Plants erect, 5–11 cm tall, branched 1.5–2.5 cm above base, many secondary branches distally at 60° angle to axis, not wandlike. **Stems** reddish-brown, glabrous, or sparsely hairy at base. **Leaves** broadly elliptic to ovate-deltate, 1.2–4 mm long, base narrowed to petiole, margins shallowly toothed or wavy, apex obtuse or broadly acute, surfaces with scattered short, white hairs. **Inflorescence** axis zigzagged, internodes 2–5 mm long, flowers not secund; bracts usually aligned with pedicel, linear, 0.8–2 mm long, base not enfolding pedicel base, apex acute. **Pedicels** diverging at 50–90° angle to axis, shallowly sigmoidally curved, 3–10 mm long, about 0.1 mm diam., tip curved up. **Flowers** resupinate; hypanthium obconic, 0.5–1 mm long, sepals slightly spreading, lanceolate to deltate (sometimes quite broad at base), 0.8–1.2 mm long, all shaped alike, 2 flanking sepals larger than the others, sinuses "u-shaped", apex acute; corolla bilaterally symmetrical, ± 1-lipped, the adaxial lobes diverging, 4–4.5 mm long, petals connate proximally 3/10–1/2, tube white, veins faintly lavender, cylindrical, (twice as long as wide), slightly narrower just below lobes, 2–2.5 mm long, abaxial surface of lobes faintly lavender at tip, adaxial surface of lobes with erect white hairs, abaxial lobes white, with yellow blotch at base, 2–2.5 mm long, central lobe elliptic, flanking lobes asymmetrically ovate, the lower margin bowed, the upper margin straight, adaxial lobes sometimes folded back, the lower margin bowed, upper margin straight; filaments erect, connate in about distal 2/3, exserted from corolla tube, white, apex densely hairy,

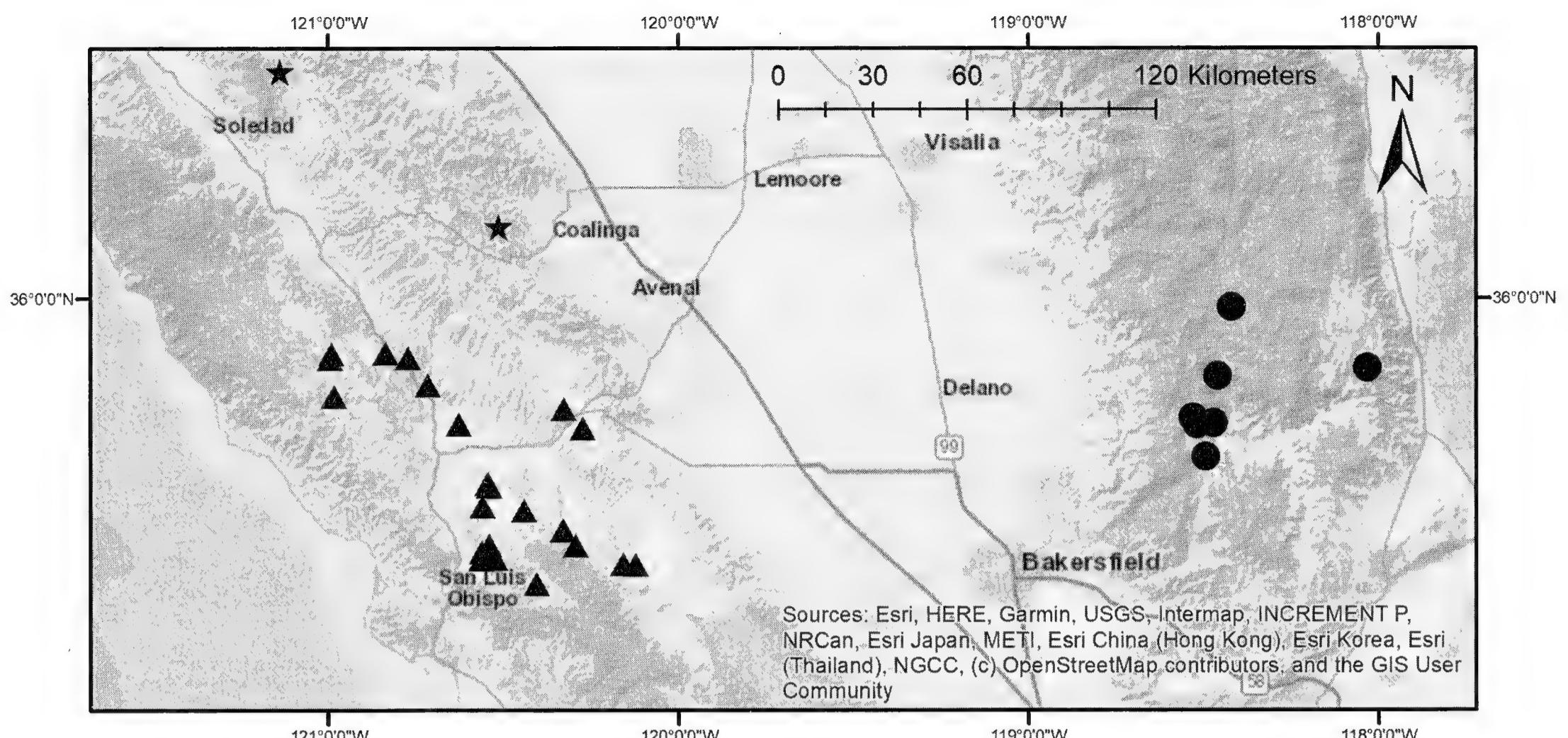


FIG. 5. Distribution of *Nemacladus secundiflorus* G.T.Robbins var. *secundiflorus* (triangles), *N. secundiflorus* var. *robbinsi* Morin (stars), and *N. bellus* (circles).

hairs moniliform, about 0.5 mm long, transparent cells 6–9 per cluster, slender, long-attenuate, sometimes held erect, attached just below connate portion of filaments to broad thick stub of tissue, anthers white to faintly lavender (about 0.4 mm long), nectary a rounded cushion at base of ovary with short, broad-based sharp-tipped hairs, ovary nearly superior, obconical. Capsule about 1/4 inferior, round, 1.5–2 mm diam., slightly oblique at base, sepals remain erect. Seeds round, 0.4–0.5 mm long, surface reticulate.

Distribution and ecology. *Nemacladus bellus* occurs on granitic gravel and sandy flats in Joshua tree woodland or mixed oak and conifer woodland, at 800–1800 m, on the Kern Plateau and in the Greenhorn Mountains of California (Fig. 5).

Phenology. Flowering May–July.

Etymology. The specific epithet, “bellus,” refers to the beautiful appearance of the plants when they are covered with delicate flowers.

Representative specimens (localities abbreviated). USA. CALIFORNIA. Kern Co.: between Isabella Dam and Keysville, Howell 51777 (CAS); Eastern Slope Sierra Nevada, along Calif. Hwy 178 E of Walker Pass, Keil & Holland 24043 (OBI). Tulare Co.: Upper part of Brush Creek Canyon on Cherry Hill Road, Howell 53758 (CAS); Kern River Canyon near Roads End Post Office, Howell 33166 (NY, CAS); Kern River Canyon north of Kernville, 0.2 miles south of intersection with Salmon Creek, Morin 626 (UC); Greenhorn Mountains ca. 5.5 miles north of Kernville, near the road to the Greenhorn Summit Store, Smith 411 (JEPS); Kern River Canyon, 5.5 miles north of Kerrville, Twisselmann 3566 (CAS, NY).

Three New Species Separated from *Nemacladus sigmoideus*

Nemacladus sigmoideus as Robbins (1958) circumscribed it occurs “in the Mojave Desert and on desert slopes of the bordering mountains, less frequent on the western borders of the Colorado Desert; Tehachapi Mountains and Mount Pinos region; east to western Nevada and Arizona; south to Lower California.” Robbins’s concept of *N. sigmoideus* was based on characters of at least four species, two of which are represented on the holotype (JEPS7686, Fig. 6). Five plants are mounted on the sheet: four have small tubular corollas and are mostly in fruit; the fifth is mostly in bud, the few open flowers being larger with corollas cup-shaped. Plants on isotypes at CAS, MO, NY, and RSA all have small tubular corollas. Robbins’s (1958) “specimens to verify range” included representatives of all three species described below, as well as *N. sigmoideus* narrowly defined, the revised description of which follows here.

***Nemacladus sigmoideus* G.T.Robbins, Aliso 4: 144. 1958.—TYPE: USA, California. Los Angeles Co., slopes of South Fork of Little Rock Creek Canyon at an elevation of 5100 feet, San Gabriel Mountains, June 14, 1953. R. Bacigalupi & G. T. Robbins 4190 (Holotype: JEPS7686!, Fig. 6; isotypes CAS!, MO!, NY!, RSA!).**

Plants erect, (6–)11–15 cm tall, basal branches at about 30° from axis, first secondary branches about 1.5 cm above base at about 70°. **Stems** brown or reddish brown, glabrous or with scattered hairs at base. **Leaves** rhombic to broadly lanceolate or elliptic, 1.5–11 × 1–5 mm, base wide, margins entire or shallowly crenate, apex obtuse or broadly acute,

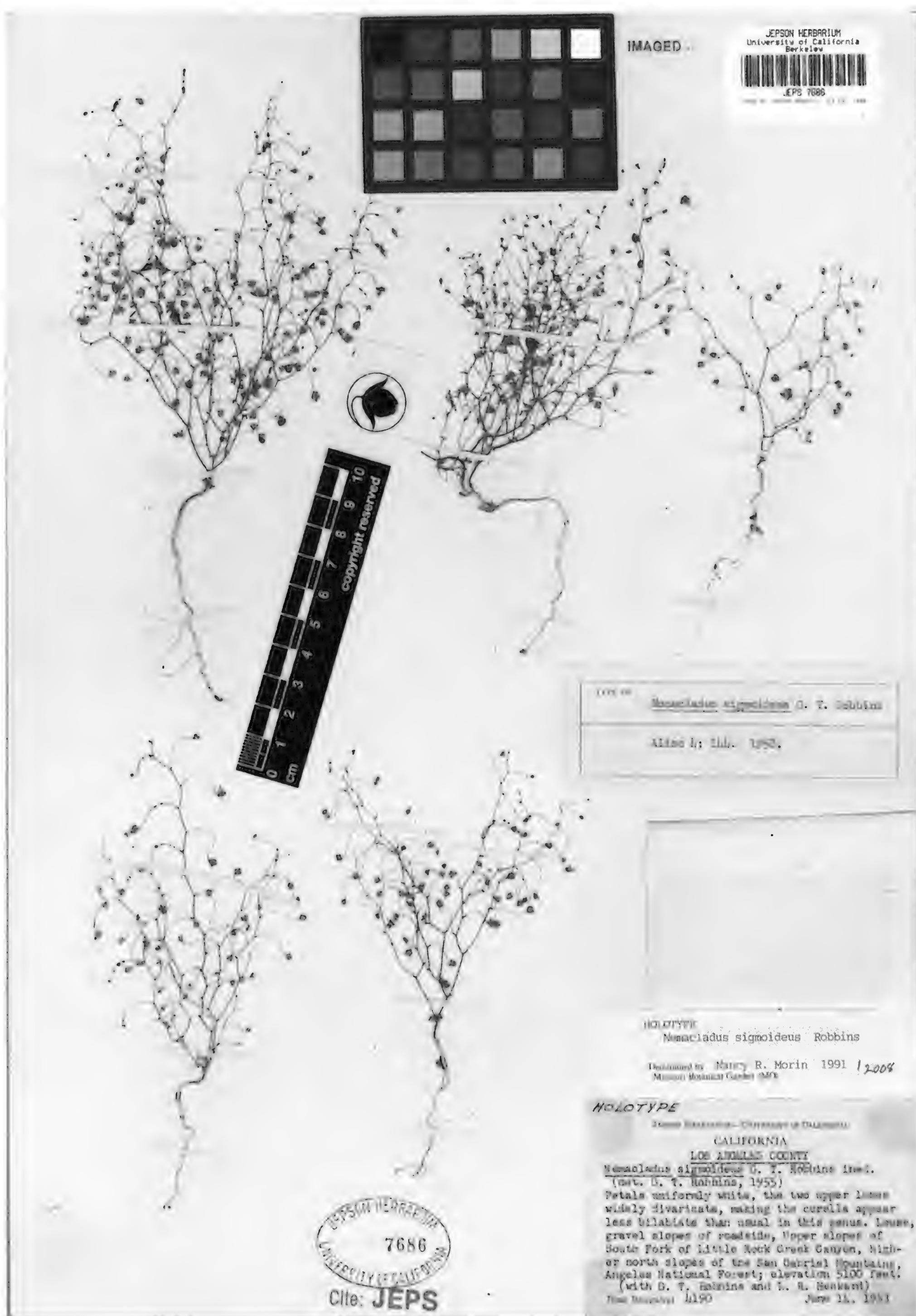


FIG. 6. *Bacigalupi & G. T. Robbins* 4190, holotype of *Nemacladus sigmoideus* G.T.Robbins. The center plant in the top row has an open flower with a cup-shaped corolla and is not *Nemacladus sigmoideus*. The other plants have smaller, tubular flowers typical of *N. sigmoideus* *sensu strictu*.

surfaces densely hairy abaxially, sparsely hairy adaxially. **Inflorescence** axis zigzagged, internodes 6–10 mm long; bracts aligned with pedicel, ovate to oblong-lanceolate, 0.8–2 mm long, base cupped around base of pedicel, apex obtuse to bluntly acute. **Pedicels** at about a 90° angle to axis, straight initially, becoming sigmoid, or deeply curved so flower is held at level of previous internode, 12–20 mm long, 0.1–0.2 mm diam. **Flowers** resupinate; hypanthium obconic, 0.8–1 × 1–1.2 mm, narrowed to base, base oblique, sepals all alike, spreading, lanceolate or broadly deltate, narrowed just at base, 1–1.3 × 0.5–0.6 mm, sinuses V-shaped; corolla bilaterally symmetrical, ± 1-lipped, the adaxial lobes divergent, petals connate in proximal 1/2–7/10, tube white, throat sometimes yellow, urceolate, 1.4–2.5 mm long, base rounded, narrowest just proximal to lobes, sometimes striate, or slipper-like, barely expanded at base, equal to or longer than the sepals, lobes white, sometimes yellow at tips, sometimes lavender abaxially, 1.8–2.5 mm long, central abaxial lobe oblong-elliptic, flanking lobes bowed on inner edge, straight on outer edge, adaxial lobes lanceolate to oblong-acute; filaments straight, slightly or well-exserted from corolla tube, connate in about distal 1/2, white or pale lavender, 1.5–2.6 mm long, abruptly bent down, somewhat constricted immediately below anthers or not, hairs at apex sparse, long, transparent cells attached just below ovary apex directly on filaments or to a narrow pad of tissue on filaments, slender, acute, anthers white or pale lavender, about 0.2 mm long; ovary about 1/2 inferior, nectaries yellow, low mounds on edge of ovary dome. **Capsules** about 2/5 inferior, almost round, 2–2.8 × 1.5–2.8 mm, base acute or oblique and flattened, apex broadly pointed, sepal tips and valve tips at about the same level or sepals longer, sepals spreading, sinus about 0.5 mm, valves and sepals widely spreading when seeds released, then sepals becoming narrower, sometimes darkening. **Seeds** widely elliptic, 0.5–0.8 mm long, surface reticulate. (Figs. 8A, B, C).

Distribution and ecology. *Nemacladus sigmoideus* occurs on sandy or gravelly soils at 200–2200 m in southern California (Fig. 7) and probably western Nevada and Arizona, south into Sonora, Mexico.

Phenology. Flowering April–June.

Specimens in a broadly defined *Nemacladus sigmoideus*, those with a small tubular corolla, sigmoid pedicel, and ovate or rhomboid basal leaves, have been collected from the southern and eastern Sierra Nevada and adjacent Nevada, Mojave Desert and northwestern Sonora Desert, Transverse Ranges, Peninsular Range, and southern Inner Coast Range. Plants most similar to the type specimen occur in the southern Sierra Nevada, Transverse Ranges, primarily on the north side, and west and north to the southern Inner Coast Range (Fig. 7). The bracts of this form are narrower than in other forms and more spreading. Their mature capsules are somewhat expanded above the hypanthium/sepal intersection,

and are surrounded by stiff, spreading, deltate sepals. The capsule valves are often shiny. Plants in the Walker Pass area of the southern Sierra Nevada have very small basal leaves and sepals that clasp the mature capsule. Also found in the southern Sierra Nevada are plants with very short corolla tubes and comparatively large capsules, and plants with long corolla tubes, both of which in other respects seem to be *N. sigmoideus*. Some plants have flowers with extremely small anthers, small enough to suggest the plants may be cleistogamous. Even given this range of variation, there are many forms that seem to have small tubular corollas, in which other aspects, such as pedicels, bracts, capsules, architecture, or basal leaves, do not fit within *N. sigmoideus* (Fig. 7, insert); although these specimens must remain annotated with this name, further study is needed to determine their true affinities.

Nemacladus sigmoideus has been confused with *N. secundiflorus* var. *robbinsii* and *N. gracilis*. *Nemacladus gracilis* has a cup-shaped corolla compared with the urceolate corolla of *N. sigmoideus*. *Nemacladus secundiflorus* var. *robbinsii* has basal leaves narrowly oblanceolate to spatulate, the margins irregularly lobed, sepals somewhat fleshy and blunt-tipped, and a cylindrical corolla tube, compared with *N. sigmoideus*, which has basal leaves rhomboid to broadly lanceolate or elliptic, the margins entire or shallowly crenate, sepals not fleshy, apex acute, and an urceolate corolla tube. *Nemacladus secundiflorus* var. *robbinsii* appears to occur only in Pinnacles National Monument, San Benito County, and Hanging Valley, Monterey County.

Representative specimens of plants closely matching the type specimen (localities abbreviated). USA. CALIFORNIA. Kern Co.: Southern Sierra Nevada Range; Piute Mountains, lower Esperanza Canyon at eastern base of Sorrell Peak and western edge of Kelso Valley, Boyd 11947 (RSA); Western Transverse Range, San Emigdio Mountains Tecuya Ridge, De Vries 7751 (RSA); Cortez Canyon, south of Bob Rabbit Canyon, Fraga 199 (RSA); Tejon Ranch, Jensen 1244, 1960, 1979, 2076, 3498 (RSA, UC); 1960 (RSA, UC); Tehachapi Willow Springs Rd, Parikh & Gale 3163, 3172, 3197, 3205 (SBBG).

Los Angeles Co.: Junction of road to Horse Flat Public Camp and main paved road from Upper Chilao Recreation Area, Bacigalupi et al. 4187 (JEPS); Mojave Desert, Hwy 138, 4 mi E of jct w Hwy 18 NE of Pinyon Hills, Boyd & Mistretta 1558 (RSA); Liebre Mtns, head of the North Fork Fish Canyon, Boyd & Raz 9817 (RSA); Transverse Ranges: San Gabriel Mountains region West terminus of Holcomb Ridge, west of Big Rock Creek, Gross 2217 (RSA); San Gabriel Mtns region, Mistretta 354 (RSA); San Gabriel Mountains, Little Rock Creek, drainage E of creek and N of Forest Rd. 4N15, Mistretta 1223 (RSA); San Gabriel Mountains region Aliso Creek, slopes W of Angeles Forest Hwy., Mistretta 5173 (RSA); San Gabriel Moun-

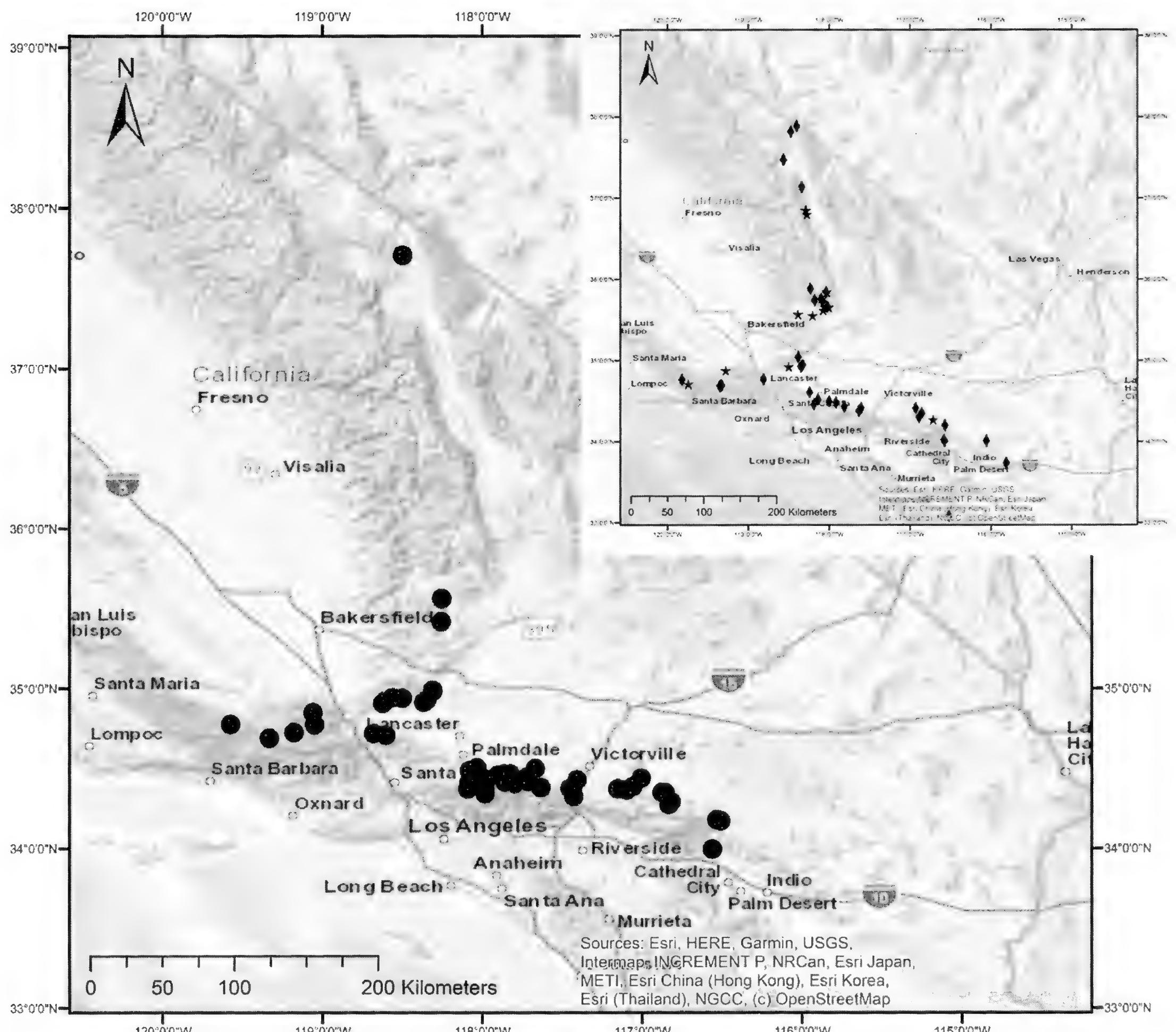


FIG. 7. Distribution of *Nemacladus sigmoideus* specimens most closely resembling type specimen (circles). Figure 7 insert. Varying degrees of resemblance to type specimen (many specimens cannot be identified yet with confidence): very probably *N. sigmoideus* (diamonds), large-capsuled *N. sigmoideus* (stars).

tains, Mill Creek Canyon, Mistretta 5241 (RSA); Little Rock Creek, north base of San Gabriel Mountains, Peirson s.n. (POM); Pinyon Ridge, between upper Little Rock Creek and the San Andreas Rift Zone, Ross *et al.* 3747 (CAS, RSA); Big Pines Hwy, midway between Caldwell Lake and Big Rock Springs, Ross & Boyd 2671 (RSA); Liebre Mountain, west summit, Ross & Boyd 7893 (CAS, RSA); Pacifico Mountain, Ross & Banks 7994 (RSA); west summit of Liebre Mountain, Ross & Boyd 8658 (CAS, RSA); San Gabriel Mountains/Mojave Desert, Mescal Highlands, Swinney 6076 (RSA, UCR); San Gabriel Mtns.; SW of Pinon Hills, Swinney 6182 (RSA, UCR); San Gabriel Mtns., nameless canyon immediately west of Jesus Canyon, Swinney 7389 (RSA, UCR); San Gabriel Mtns., Devils Punchbowl Co. Park, Swinney 8927, 8938 (UCR); San Gabriel Mtns. Sulphur Springs Campground, Swinney 10955 (RSA, SD, UCR); San Gabriel Mountains, NNE of

Oracle Hill Summit, Swinney 12841 (UCR); Transverse Ranges; San Gabriel Mountains, N of Bob's Gap, Thorne 43469 (MO, RSA, UC); San Gabriel Mountains region, North of Shoemaker, Thorne 43511 (MO, RSA, UC); San Gabriel Mts., Juniper Hills, c. 2 mi S of Ft Tejon Road, Thorne 43524 (RSA); Mojave Desert Slope, Junction of Pallett Creek & Longview Road, Thorne 43410 (MICH, RSA); San Gabriel Mountains, near Shoemaker Canyon, Vanderplank *et al.* 50506 (RSA); San Gabriel Mts., Juniper Hills, Wheeler s.n. (RSA); San Gabriel Mtns. Mill Creek Summit, Wood 789 (RSA); San Gabriel Mountains, Vicinity of Little-rock creek; Wood 1623b (RSA). **Riverside Co.:** Dry Morongo Wash, nw end of Coachella Valley, Munz 16239 (NY, RSA). **San Bernardino Co.:** Mojave Desert along Pioneertown Road, just west of Black Hill, André 17163 (UCR); The Pioneertown Mountains Preserve, Bell 6607 (RSA); 6 mi w of Hesperia,

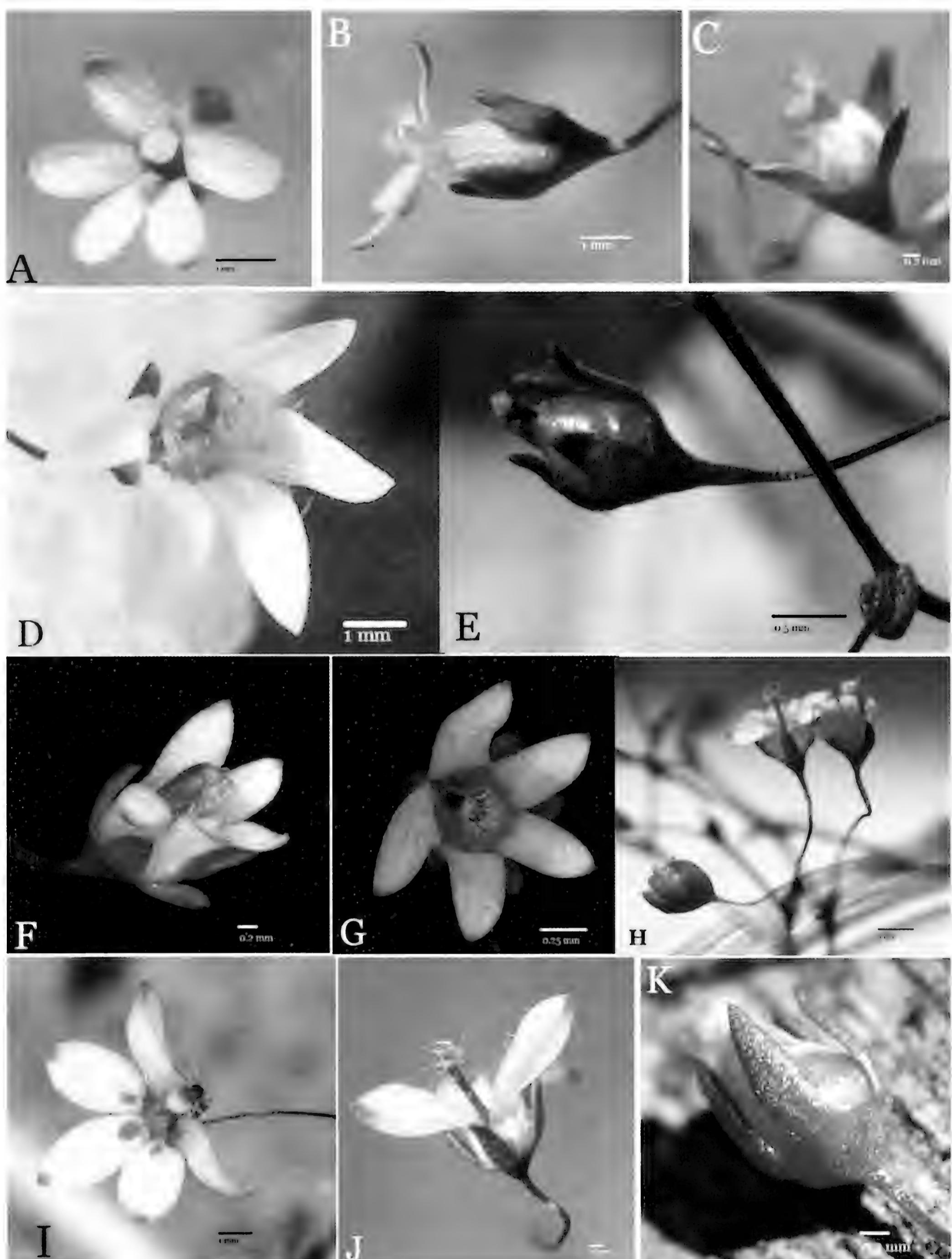


FIG. 8. *Nemacladus* flower and capsule comparisons: *Nemacladus sigmoideus*: A. flower front view. B. flower top view. C. capsule. *Nemacladus parikhiae*: D. flower, front view. E. capsule. *Nemacladus eastwoodiae*: F. flower side, G. flower front, H. flower top and side, and capsule. *Nemacladus matsonii*: I. flower front, J. flower top, K. capsule (photos: A, B, C, D, E, H, K, N. Morin; F, G, T. Ayers; I, J, S. Matson).

Johnston (POM,); Cushenbury Canyon., *Morin* 617 (UC); Cajon Pass, *Parish & Greata* 1931 (RSA); Baldwin Lake, *Peirson* 6747 (DS, RSA); Cajon Summit, *Sanders* 6502 (UCR); San Bernardino Mts, wash below Rattlesnake Spring, *Sanders* 17091 (UCR); Mojave desert: Baldy Mesa, north of Cajon Summit, *Sanders* 21791 (UCR); Pinyon Hills, ridge-top E of Oak Springs Canyon, *Swinney* 3968 (RSA, UCR); Transverse Ranges; Baldwin Lake: W end of lake, *Thorne* 52284 (RSA); San Bernardino Mtns. relay station on Grapevine Canyon Road, *Thorne* 53027 (RSA); 1 mi ENE of Bowen Ranch, *Thorne & Prigge* 52915 (RSA); S of Lucerne Valley on alluvial slope below Pfizer limestone quarry in Marble Canyon, *White s.n.* (UCR). **Santa Barbara Co.:** east end of San Rafael Mountains, upper reaches of Santa Barbara Canyon, south from the mouth of Alamo Canyon, *Gross* 3383 (RSA); Big Pine Basin, San Rafael Mountains, *Hoffmann s.n.* (SBBG). **Ventura Co.:** Near summit of grade along road south of and overlooking Lockwood Valley, *Bacigalupi* 4522 (JEPS); Near Camp Ozena, *Chandler* 3500 (MO); Lockwood Valley Road west of Seymour Creek, *Morin* 578 (UC); Camp Ozena, *Morin* 579 (UC).

The fifth plant on the type specimen of *Nemacladus sigmoideus* is placed here in *Nemacladus parikhiae*.

Nemacladus parikhiae Morin & T.J.Ayers, sp. nov.—

Type: USA, California, Los Angeles Co., Slopes W of Angeles Forest Hwy about 0.6 mi N of jct with Aliso Cyn Rd, 34.43411°N, 118.09149°W. Alt. 1189m/3900ft. Coarse soils, full sun. Former chaparral/scrub association, completely burned in Station Fire in 2009. Currently rich assemblage of mostly native annuals and seedling/stump sprouting perennial shrubs and trees, including *Mentzelia veatchiana* Kellogg, *Gilia modocensis* Eastw., *G. ochroleuca* M.E.Jones, *Cryptantha muricata* var. *jonesii* (A.Gray) I.M.Johnst., *Chaenactis glabriuscula* DC., *Poa secunda* J.Presl., *Eriodictyon crassifolium* var. *nigrescens* Brand, *Lotus strigosus* (Nutt.) Brouillet, *Lupinus bicolor* Lindl., *Ericameria linearifolia* (DC.) Urbatsch & Wussow, *Claytonia parviflora* Hook., *Adenostoma fasciculatum* Hook. & Arn., *Cercocarpus betuloides* Nutt. Uncommon, Corolla irregular, 20 May 2010. *Orlando Mistretta* 5160 with *Christine Mistretta* (Holotype: RSA777928!, Supplemental Fig. 4; isotype SFV).

Nemacladus parikhiae differs from other *Nemacladus* in having a 2–4 mm long, cup-shaped, bluetinged corolla, the filament tube dark purple to reddish purple distally, transparent cells very slender, tapered; anthers dark blue, 0.2–0.3 mm, empty anthers gray (Figs. 8D, E).

Plants 5–12 cm tall, branches from base and 1–2 cm above, at 45° to axis or more, secondary branches at 50–60°. **Stems** reddish brown, glabrous or with scattered hairs. **Leaves** broadly deltate to elliptic, 2–

4.5 × 1.7–1.8 mm, base broad, abruptly or gradually narrowed, margins toothed, apex acute, surfaces glabrous. **Inflorescence** axis slightly zigzagged, internodes 2.5–5 mm long; bracts aligned with pedicel but not clasping, narrowly ovate, 1–1.2 mm long. **Pedicels** 6–18 mm long, about 0.1 mm diam., at about 90° to axis, straight to shallowly curved, tip curved up. **Flowers** resupinate; hypanthium broadly obconic, 0.5–0.6 mm long, sinuses flat, sepals erect, deltate, 0.5–1 mm long; corolla bilaterally symmetrical, 1-lipped, the adaxial lobes divergent, petals connate 1/10–1/4 proximally, white with a faint blue tinge, with dark pink or greenish veins, 2.5–4 mm long, tube broadly cup-shaped, about 0.5–1 mm long, slightly gibbous at base, medial sinus slit nearly to base, ovary dome clearly visible, pentagonal, green, corolla lobes 2–3 mm long, long hairs scattered adaxially, 1.2–2 mm long, abaxial lobes elliptic, acute, adaxial lobes slightly asymmetrical, oblong, acute, folded back; filaments connate nearly to base, arched over, dark purple to reddish purple distally, abruptly curved at tip, few very long hairs at apex, transparent cells numerous (10+ per group) attached to pad at base of filaments, very slender, attenuate, anthers dark blue, 0.2–0.3 mm long, empty anthers gray; ovary about 3/4 inferior, nectaries pale yellow or pale green. **Capsule** ellipsoid, 0.8–1.5 × 1.6–3 mm, base oblique, narrow, apex narrow, sepals erect or flared outward from middle. **Seeds** oblong-elliptic, 0.5–0.6 mm, surface reticulate.

Distribution and ecology. *Nemacladus parikhiae* occurs in chaparral and creosote bush scrub on coarse gravelly soils at 800–1800 m. It is found in the Transverse Ranges, with gaps in distribution between the western San Gabriel Mountains, Los Angeles County, the San Bernardino Mountains, San Bernardino County, and San Jacinto Mountains, Riverside County (Fig. 9).

Phenology. Flowering (March) April–July.

Etymology. *Nemacladus parikhiae* is named in honor of Dr. Anuja Parikh, who, with Nathan Gale, for years has provided extremely helpful photos, specimens, and observations of many *Nemacladus* taxa. They have done the same for many other genera and Southern California botanists, including rediscovery the San Fernando Valley spineflower, *Chorizanthe parryi* var. *fernandina* (S.Watson) Jeps. at Newhall Ranch (Spratt 2018). We are very grateful to both of them for their help with *Nemacladus*.

Representative specimens (localities abbreviated). USA. CALIFORNIA. **Los Angeles Co.:** Mount Wilson, *Abrams* 1899 (NY, DS, POM RSA); 4 miles northeast of Lancaster on the Muroc Road, *Ferris* 9480 (DS, GH, ORE); Upper Big Tujunga Canyon, 0.3 km ENE of Shortcut Station, 0.7 km N of State Highway 2 (Angeles Crest Hwy), *Anuja Parikh*, *Nathan Gale* 3595 (SBBG); from alder saddle along s. fork Little Rock Creek, *Gross* 2385 (RSA); San Gabriel Mtns: Mill Creek Canyon, near spur road to

falcon Mine, *Mistretta* 5223 (RSA); San Gabriel Mountains region North Fork Mill Creek, *Mistretta* 5296 (RSA, UC); Western extension of Waterman Mountain, along Waterman Mountain trail, *Soza* 1683 (RSA); near Chilao Creek, Upper Chilao Campground, *Thorne* 38285 (RSA); Big Tujunga, ridge E of Coldwater Canyon, *Wheeler* 6641 (RSA). **San Bernardino Co.:** Sawtooth Mountains, *Bell* 1136 (RSA); Bighorn Mountains 1.25 air miles nw of Viscera Spring, *Bell* 6769 (RSA); Burns Canyon, *Morin* 644 (UC); mouth of Burns Canyon, 0.5 mi W of end of pavement near Rimrock, *Sanders* 12279 (UCR); 2.1 mi above Rimrock Rd just below Burns Springs, *Sanders* 16861 (UCR).

A population from Aliso Canyon, San Gabriel Mountains, Los Angeles County (Parikh & Gale 3485) with small, lavender tinged, nearly actinomorphic, cup-shaped corollas and dark purple filament tips may be a small-flowered version of *N. parikhiae*. More study is needed to determine whether plants with flowers like *N. parikhiae*, but with paler filaments and long, upwardly curved pedicels and large capsules found in the Lake Arrowhead and Bear Lake region warrant recognition. At least at Crab Flat, east of Lake Arrowhead, San Bernardino Mountains, this form grows with *N. sigmoideus* s.s. in some years. Representative collections of these are: 3.5 air miles east of junction of Pacific Crest Trail and forest service road 1N05, *Bell* 1377; Bighorn Mountains, central Ruby Canyon, *Bell* 6681 (RSA); San Bernardino Mountains region; FS Rd 3N34, on the slopes above Hooks Creek, just east of its confluence with Bear Creek, *Fraga* 1619 (RSA); San Bernardino Mountains region, on Pacific Crest Trail, 0.25 mi N of FS Road 2N04, east of YMCA camp, Camp Oaks, near Arrastre Creek, *Fraga* 2171 (RSA); San Bernardino Mountains region; West of South Fork Campground, north of Hwy. 38 & Santa Ana River, *Gross* 1139 (RSA); N of Baldwin Lk, 0.8 mi W of Smart's Ranch, *Sanders* 17304 (UCR); Barton Flats area, Hathaway Flat along Glass Road, near Barton Creek, *Sanders* 17370 (UCR); San Bernardino Mtns., Little Bear Creek, c. 1.5 mi. ENE of Lake Arrowhead, above confluence with Hooks Creek, *Sanders* 28342 (UCR).

Although G. T. Robbins (1958) considered all plants in the Mojave Desert and adjacent regions with sigmoid pedicels and very small white corollas to be *Nemacladus sigmoideus*, these can be resolved into two distinct groups—those described in the more narrowly circumscribed *N. sigmoideus* as usually having entirely white or pale lavender, tubular corollas and white or pale lavender filaments and anthers, and plants with white or cream-colored, cup-shaped corollas, the throat and lobes yellow-tipped, filaments maroon distally, and gray or white anthers, described here as *N. eastwoodiae*.

***Nemacladus eastwoodiae* Morin & T.J.Ayers, sp. nov.**—Type: USA. California. San Bernardino Co., Mesquite Mountains, Winter's Pass. Sandy

wash with *Larrea tridentata* (DC.) Coville, *Yucca schidigera* Roezl ex Ortgies, *Y. baccata* Torr., *Salvia dorrii* (Kellogg) Abrams, *Hymenoclea salsola* Torr. & A.Gray [=*Ambrosia salsola* (Torr. & A.Gray) Strother & B.G.Baldwin], *Acacia greggi* A.Gray [=*Senegalia greggii* (A.Gray) Britton & Rosei, *Eriophyllum wallacei* (A.Gray) A.Gray, *Camissonia brevipes* (A.Gray) P.H.Raven [=*Chylismia brevipes* (A. Gray) Small], *Nemacladus* spp., *Salazaria mexicana* Torr. [=*Scutellaria mexicana* (Torr.) A.J. Paton], *Dyssodia cooperi* A. Gray [=*Adenophyllum cooperi* (A. Gray) Strother], *Mimulus bigelovii* A. Gray [=*Diplacus bigelovii* (A. Gray) G.L. Nesom], *Eriogonum inflatum*, etc. Delicate annual, 3500 ft. May 10, 1978. *Thorne et al.* 51354 (Holotype: RSA 275909!, Supplemental Fig. 5; isotype MO!).

Nemacladus eastwoodiae differs from other *Nemacladus* in having a combination of small, 1–1.6 mm, cup-shaped corollas, maroon filaments, white or gray anthers, very long, slender, deeply curved pedicels, and sepals clasping the capsules, which bear few, relatively large seeds (Figs. 8F, G, H).

Plants erect, (4)–8–12 cm tall, branches from base at 30–50° from main stem and 1.5 cm above at 60–70°, secondary branches many, at 40–50°, tertiary branches few, at 40–50° angles. **Stems** light brown or reddish brown, glabrous. **Leaves** rhombic to elliptic, 3–6 × 1.5–2 mm, base narrowed, margins sharply but shallowly toothed, apex acute, surfaces glabrous or pubescent. **Inflorescence** axis ± shallowly zig-zagged, internodes 4–6 mm long; bracts straight or arched back, aligned with pedicel, narrowly lanceolate, 1–1.6 mm long, base enfolding pedicel base, apex acute. **Pedicels** 10–15 mm long, <0.1 mm diam., at least 2x longer than internode, much thinner than axis, 90° to axis, deeply sigmoidally curved, tip erect. **Flowers** resupinate; hypanthium green, obliquely obconic to hemispheric, (0.4)–0.5–0.6 mm long, sepals erect, ± alike, oblong-deltate, 0.6–1.2 mm long; corolla bilaterally symmetric, ± 1-lipped, petals connate in proximal 1/4, tube cup-shaped, wider than deep, 0.2–0.4 mm long, lobes white or cream-colored with yellow tips and throat, oblong elliptic, 0.8–1.2 mm long, with scattered long hairs adaxially, 3 abaxial lobes spreading, 2 adaxial lobes divergent and folded back; filaments connate in distal 1/2, tube maroon distally, connective maroon, 1–1.3 mm long, transparent cells narrowly deltate, attenuate, attached to a short stalk connected near the base of the filaments, anthers white or gray, 0.15–0.2 mm long, pollen white; ovary 1/2 inferior, nectaries greenish yellow, low mounds on edge of ovary dome. **Capsule** 1/4 or less inferior, straw-colored, round, 1–2 × 1–2 mm tall, base acute, apex rounded, abaxial sepal remaining cocked, adaxial sepals clasping the capsule, sinuses U-shaped, valves ultimately opening widely. **Seeds** elliptic, 0.5–0.6 mm long, surface reticulate.

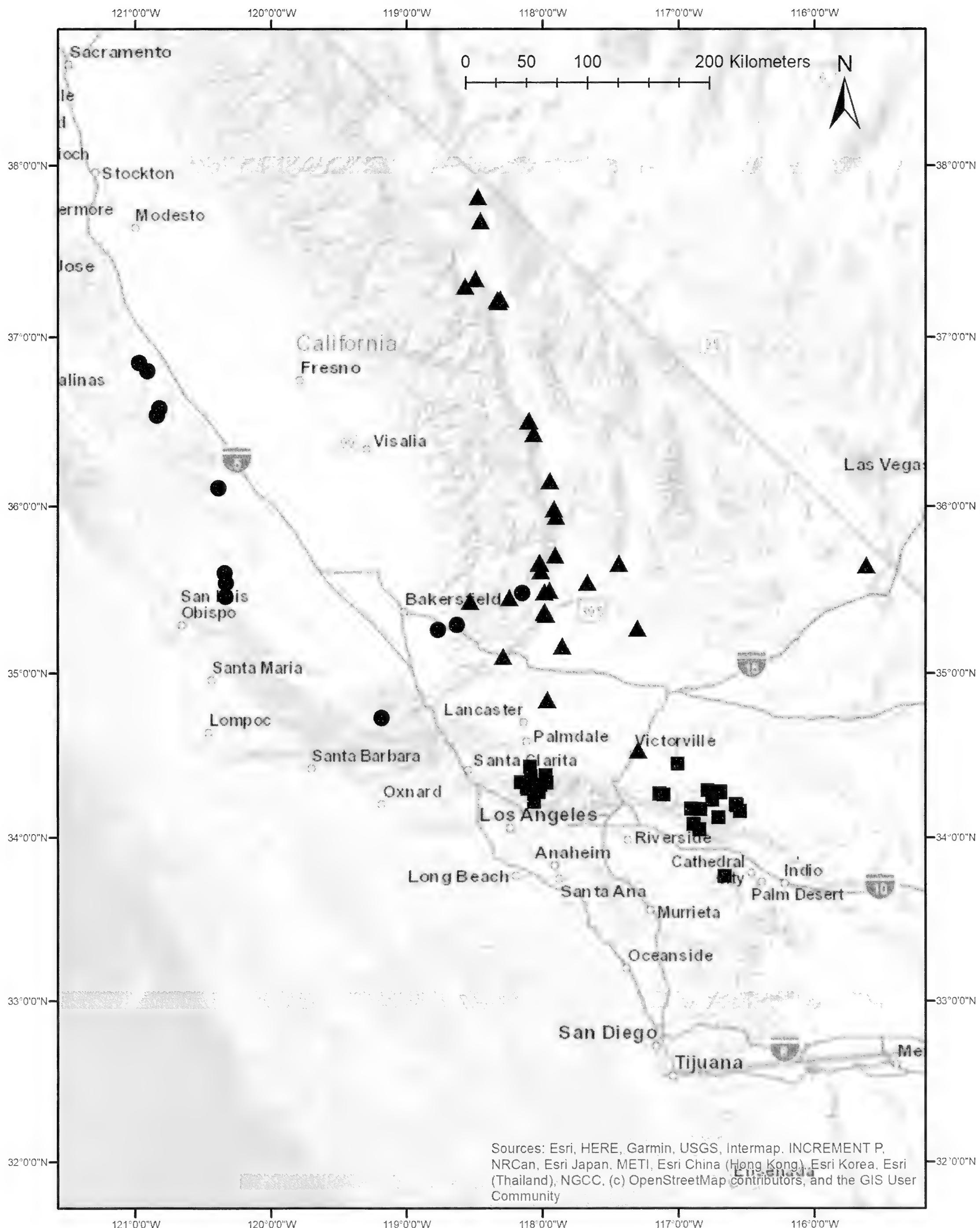


FIG. 9. Distribution of *Nemacladus matsonii*-(triangles), *N. parikhiae*-(squares), and *N. gracilis*-(circles).

Distribution and ecology. *Nemacladus eastwoodiae* occurs in sandy washes and openings, on rocky slopes, in Joshua Tree woodland, and creosote bush scrub; at 900–2200 m, in California and Nevada, primarily in the Mojave Desert and Owens Valley (Fig. 10).

Phenology. Flowering April–June.

Etymology. *Nemacladus eastwoodiae* is named for Alice Eastwood, 1859–1953, quintessential California botanist, who collected *Nemacladus* throughout the

state. She collected *N. eastwoodiae* near Baker, San Bernardino County, with Tom Howell; this locality is where the senior author first saw this lovely plant.

Similar species. Although very similar to *N. sigmoideus* in its sigmoid pedicel and broad basal leaves, *N. eastwoodiae* can be distinguished on herbarium specimens because the filament tube often is extended above the corolla and generally is still visible above the dried corolla, whereas in *N. sigmoideus* the filament tube is wrapped in the remains of the corolla.

Nemacladus tenuis (McVaugh) Morin var. *tenuis* also has small white corollas and can be distinguished from *N. eastwoodiae* in having the two adaxial lobes tipped with reddish brown, the three abaxial lobes with a deep rose chevron, and deeply toothed or pinnately lobed leaves.

Selected specimens (localities abbreviated). USA. ARIZONA. Mohave Co.: 7 miles southeast of Yucca, *Gould & Darrow* 4312 (UC, CAS, ARIZ). CALIFORNIA: Inyo Co.: Sierra Nevada Mtns., Big Pine Canyon, along Glacier Lodge Road, *André* 11660 (UCR); About 22 miles south-southeast of Olancha, *Henrickson* 17922 (RSA, CHICO, NY, TEX); Desert flats, *Robbins* 3488C (JEPS). Kern Co.: Branch Park, 1 mi N and 1 mi W of South Gate to Edwards AFB, *Charlton* 5332 (RSA); W Mojave Desert, *Hoffmann* s.n. (SBBG); 0.8 km N of Tehachapi Willow Springs Rd, just W of 100th St West, *Parikh & Gale* 3173 (SBBG); south end of Soledad Mountain, *Twisselmann* 4312 (CAS); Rademacher Hills, Summit of Hwy 395, *Twisselmann* 7063 (CAS); El Paso Mountains: Last Chance Canyon, *Twisselmann* 4354 (CAS, JEPS); Mojave-Randsburg Region, *Twisselmann* 4439A (JEPS). Los Angeles Co.: Lancaster, *K. Brandegee*, s.n. (POM); Transverse Ranges, San Gabriel Mtns. region, *Mistretta* 600 (RSA); Transverse Range; San Gabriel Mtns./Western Mojave Desert Carr Canyon, *Swinney* 10596 (UCR); Transverse Range; San Gabriel Mtns., lower Brainard Canyon, *Swinney* 10749 (UCR). San Bernardino Co.: Monkeyflower Wash s of Kane Wash, N Ord Mtn area, *André* 5112 (UCR); Ivanpah Valley, *André* 12777 (RSA); southwest of Cima dome along Mojave Road at Cedar Wash, *André* 14658 (UCR); Old Woman Mountains, north end of range at historic Enterprise Mine area, near corral, *André* 24903 (RSA); Kelso, *Baldwin* 256 (RSA); Turquoise Mountains about 2.75 air miles north of Halloran Spring, *Bell* 4845 (RSA); Pioneertown Mountains Preserve; Pipes Wash, between Black Hill and Flat Top, *Bell* 6734 (RSA); *Bell* 7972 (RSA); *Bell* 6538 (RSA); Kingston Wash at Coyote Holes, *Castagnoli et al.* 99 (RSA); Mohave Desert, along Hwy 18, ca. 0.5 mi E of jct w/ Hwy 66–91, *Davis* 130 (UCR); At turnoff to the Fossil Pit road from the paved highway, *Dunn* 5611 (UCR); near Baker, *Eastwood & Howell* 8895 (CAS); Halloran Summit exit on Interstate 15 in the Mojave Desert, halfway between Barstow and Las Vegas, *Ertter* 9957 (UC); Mojave Desert, *Hall* 6819

(UC (w/ *orientalis* and an odd *rubescens*)); Eastern Mojave Desert large wash crossing Kelbaker Road 5 mi north of Kelso, *Helmkamp* s.n. (UCR); Garlic Springs, *Hoffmann* s.n. (SBBG); half way between Adelanto and Johannesburg, Mohave Desert, *Jaeger* s.n. (POM); 15 mi S of Warren's Well, Little San Bernardino Mts., *Jaeger* s.n. (POM); Stoddard Well, *Jepson* 5915 (JEPS); Barstow, by Iverson Hill, *Jepson* 17188B (JEPS); Barstow, *Jepson* 5822 (JEPS, NY); Mojave Desert, *Jepson* 20509 (JEPS); 5.5 miles northeast of Kelso, *Jepson* 20573 (JEPS); Along road to Baker on mountain slopes above Kelso, *Jepson* 20585 (JEPS); Mojave Desert, *Jepson* 20512A (JEPS, MICH, US); SE of Victorville, *Johnston* s.n. (POM); Along Wildhorse Canyon Road, *Junak* 1176 (SBBG); Near Calico, *Lemmon* s.n. (UC); Transverse Ranges; Santa Ana River Canyon, Junction of Stetson Creek Road (Forest Road 1N36) and Round Cienega Creek, *Mistretta* 3795 (RSA); 20 mi. N of Box "S" Ranch, *Munz* 12440 (UC, POM); South base of Sugarloaf Mountain, *Munz* 17118 (POM); 3 mi E of Warrens Well, *Munz & Johnston* 5191 (POM); New York Mts. e Mojave Desert, *Prigge* 2879 (RSA); Kramer Hills, *Roos* 5634 (RSA, UCR); 3.9 mi E of the Field Rd. exit on I 15, ca. 7 mi NW of Afton Cyn., *Sanders* 256 (UCR); Mojave Desert/San Bernardino Mtns; north foot of mtns below the Partin Brothers Mine (Terrace Springs), 4.6 mi. SSW of Old Woman Springs Road, *Sanders* 16927 (UCR); Eastern Mojave Desert Ivanpah Valley, alluvial slopes below Clark Mountain, *Sanders* 38165 (UCR); Southeastern end of the Kingston Range. 6.8 miles northwest of Kingston road on Excelsior Mine road, *Sanders* 263 (SBBG, UCR); Cushenbury Canyon, off Hwy 18 to the west near Cal Trans 5000 ft elevation sign, *Soza et al.* 233a (RSA); Mojave Desert; Southcentral Mojave Desert region New Dixie Mine Road, *Stoughton et al.* 1258 (RSA); Riggs Wash, south of Kingston Range Wilderness on C0743, approximately 10 miles E/NE of Hwy127, *Stoughton et al.* 1320 (RSA); Mojave Desert; S of Hwy 247 in Johnson Valley, *Swanson* 534 (RSA); Mojave Desert; East Mojave Desert region New York Mountains, *Thorne* 51311 (RSA); Mojave Desert, Mesquite Mountains, Winter's Pass, *Thorne* 51354 (RSA); Lucerne Valley, 0.3 miles west of Lucerne Valley, *Thorne* 51796 (RSA); Southcentral Mojave Desert 1 mi SW of S end of Rabbit Dry lake, *Thorne* 53034 (UCR); Southeast end of Kelso Sand Dunes. 7 miles south of Kelso on Amboy Road, *Wolf* 10214 (CAS, NY, RSA); Excelsior Talc Mine, *Wolf* 10383 (DS, RSA); San Bernardino Mountains Ridgeline west of Mohawk Mine, *Wood* 2002 (RSA). NEVADA. Esmerelda Co.: Oriental Wash, 0.4 road miles ENE of junction with Tule Canyon Road, *Tiehm* 14657 (CAS, NY, UTC). Lincoln Co.: Kane Springs Valley, Kane Springs Wash 9 road mi NE of hwy 93 on road to Elgin, *Tiehm* 7638A (CAS, NY, USA). Nye Co.: Nevada Test Site, *Beatley* 12842 (RSA, UNLV).

Photographs in CalPhotos by Steve Matson (2010) alerted the authors to the following new species. Thomas Howell and Ernest Twisselmann both collected *N. sigmoideus*-like plants with large corollas, maroon filaments, and white anthers extensively. Twisselmann on his collection number 3536 noted the maroon filaments and bright white anthers. Heller, on his collection number 8878, noted that the plants might be distinct.

***Nemacladus matsonii* Morin & T.J.Ayers, sp. nov.—**

Type: USA, California, Inyo Co., 9 miles sw Lone Pine (Carrol Creek Pack Station). Sandy desert. 5500 ft. May 25, 1958. *Lewis S. Rose* 58072 (holotype: UC 1106156!, Supplemental Fig. 6; isotypes DS!, GH!, MO!, NY!, RSA!, US!, WTU!).

Nemacladus matsonii differs from other *Nemacladus* in having the combination of a large flower, 3.5–5 mm, the corolla tube cup-shaped, the medial sinus deeper than the others, the lobes cream-colored with a yellow splotch at the base, the filament tube and connective red to faded magenta, the anthers white or cream-colored. (Figs. 8I, J, K.)

Plants erect, (2.5)–7–16 cm tall, branched from base and 1–1.5 cm above base, at lowest 1–3 nodes, secondary branches numerous, branch angles wide, (60)–85–90° to main stem. **Stems** dark red, glabrous or with scattered hairs. **Leaves** ovate, elliptic, lanceolate, to obovate, 2–8 × 1.5–4 mm, base narrowed, margins entire or teeth very shallow, apex obtuse or acute, surfaces glabrous abaxially or sparsely hairy, densely hairy adaxially. **Inflorescence** axis zig-zagged, internodes 4–8 mm long; bracts mostly aligned with pedicel, or bent back, narrowly lanceolate to ovate, 1–2.5 mm long, base folded against but not around pedicel base, apex acute, surface hairy abaxially, the hairs white. **Pedicels** at 80–110° angle to axis, 8–18 mm long, 0.1–0.15 mm diam., sigmoid, proximal portion straight or curve broad, distal curve abrupt (zigzag of axis amplifies width). **Flowers** resupinate; hypanthium broadly obconic, 0.3–0.8 mm long, sepals slightly spreading, ± alike, lanceolate, 0.7–1.5 mm long, apex acute, sinus broad, straight, adaxial sepal cocked back, sepals longer than corolla tube; corolla bilaterally symmetric, ± 1-lipped, 3–4.5 mm long, tube cream-colored, cup-shaped, length equal to or less than width, medial sinus deeper than other sinuses, lobes cream-colored with yellow splotch at base, tip cream-colored or yellow, drying darker, 2.2–4.5 × 0.6–0.7 mm, apex acute, with white, erect hairs on adaxial surface, hairs about 0.1 mm long, central abaxial lobe spatulate-elliptic, flanking lobes elliptic, adaxial two lobes straight on upper (adaxial) edge, slightly bowed on lower edge; filaments connate entire length, tube straight then curved over, tube and connective red to faded magenta, 1.1–2 mm long, apex with sparse moniliform hairs, transparent cells broadly deltoid, base broad, tip pointed, attached to a broad pad of tissue that is attached at the level of the ovary apex, anthers white or cream-colored, 0.4–0.6 mm long,

shiny, pollen cream-colored; ovary elongated, almost superior; nectaries yellow, round, on wall of ovary near base. **Capsules** 1/5–3/10 inferior, darkish, becoming straw-colored, round or broadly ovoid, 2–3 mm diam., base rounded or oblique, apex rounded, sepals erect to slightly spreading, with wide, flat sinuses, valves broad, translucent, sepals and valves erect in open capsules. **Seeds** oblong, 0.5–0.6 × 0.3 mm, surface with wavy ridges separated by large cells.

Phenology. Flowering April–June.

Distribution. *Nemacladus matsonii* occurs on compact sand and stabilized dunes, in Joshua tree woodland and creosote bush scrub, at 700–1700 m in the Owens Valley south through the Red Rock Canyon area to at least the Tehachapi Mountains. (Fig. 9.)

Etymology. The species is named in honor of Steve Matson, who has been documenting the plants of the western U.S., especially the Owens Valley, making his excellent images (nearly 24,000) available through CalPhotos (<http://calphotos.berkeley.edu>).

Representative specimens (localities abbreviated). USA. CALIFORNIA. Inyo Co.: Owens Valley along transmission line road, c. 4 miles north of Big Pine, 1 mile east of Hwy 395, 0.5 mi. north of Klondike Reservoir, André 11548 (RSA, UCR); near Oak Creek Campground just N of Whitney Fish hatchery, André 11641 (UCR); Eastern Sierra Nevada Cottonwood Creek, Wormhole Canyon, along Cottonwood Road, 2.1 mi west of US Hwy 395, c. 11 mi north of Olancha, André 17882 (UCR); Little Lake, south of cinder cone, sandy soil, elev. 3500 ft, DeDecker 2041 (RSA); Owens Valley: 3.5 mi N of Big Pine, DeDecker 3450 (RSA); Near Little Lake, Hall 7362 (UC, UNLV, POM); Foothills west of Bishop, Heller 8278 (CAS, DS, GH, JEPS, NY, UC, US); About 23 air miles south-southeast of Olancha, Henrickson 18058b (CHICO, NY, RSA); 6 mi SW of Bishop along Hwy 168 near 5000' elev. sign, along dirt road N of Highway, broad decomposed granite sand and gravel alluvial fan, Honer 2321 (RSA); on road from Lone Pine to Whitney Portal road, 6500', Howell 33310 (CAS); Carroll Creek, morainal slopes, Howell 33372 (CAS, MO, NY); north of Big Pine near power transformers, Morin 683 (UC); Bishop Highway 3.8 mi N of Big Pine, Twisselmann 15537a (CAS); 3.25 mi e of US Hwy 395 and 3.5 mi s of Coso Rd., Zembal CHSA 196, with *N. sigmoideus* (RSA). Kern Co.: Gravelly wash at north end of Walker Basin at crossing of road to Havilah, Bacigalupi 4528 (CAS, DS, GH, JEPS, RSA, SLO). Tehachapi Pass, Piute Mountain Range, Benson 3500 (RSA, US, WTU); E of Mojave, Carter and Kellogg 3167 (UC); Red Rock Canyon, Dearing 4637 (SBBG); Owens Peak eastern watershed, Short Canyon, Fraga 1099 (RSA, UC); Mojave Desert, California City land development, Holmgren & Holmgren 7689 (CAS, NY); 5 miles east of Claraville, Howell s.n. (CAS); 8 miles north of Ricardo, Kern Co., Howell 4997 (CAS); East side of Walker Pass, Howell 37206 (CAS, MO); Southern Sierra Nevada, Scodie Mtns, Kiawah Wilderness, Cow

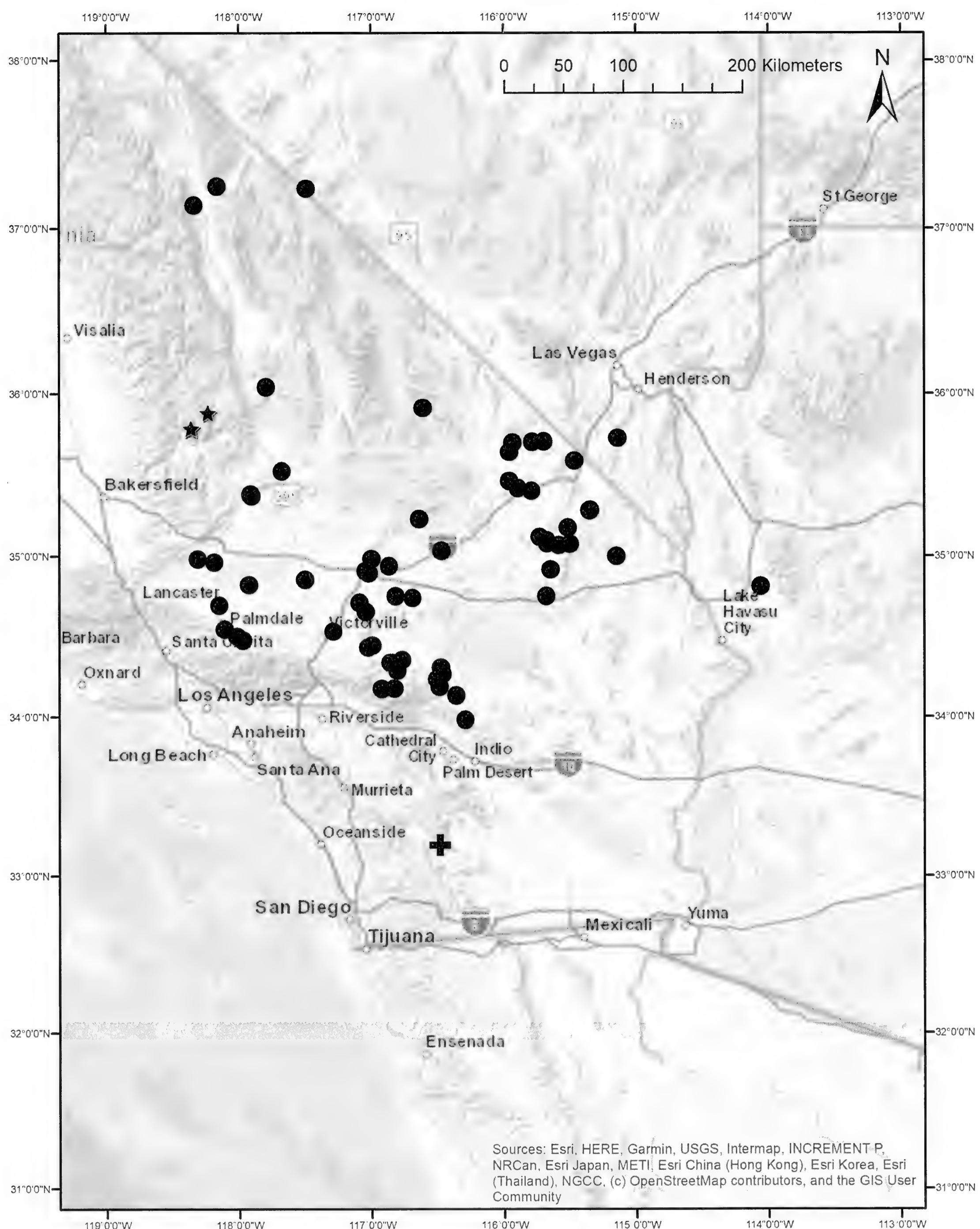


FIG. 10. Distribution of *Nemacladus eastwoodiae* (circles); *Nemacladus twisselmannii* var. *twisselmannii* (stars) and *N. twisselmannii* var. *botanywomaniae* (cross).

Haven Canyon, west side of the main road, Gardner & Poutasse 833 (RSA); Mojave, Jones s.n. (UC, US); Sandy flats, 9 mi. north of Ricardo, Munz 12463 (POM, UC); 0.5 miles east of summit of Walker Pass, Munz 13362 (POM, RSA, WTU); 8 mi n of Ricardo,

Indian Wells Valley, Peirson 8821 (RSA); Walker Pass, e slope, Rose 62040 (CAS, JEPS, MICH, RSA); East fork of Red Rock Canyon, Twisselmann 3536 (CAS, JEPS); East slope of Walker Pass, Twisselmann 4497 (with *N. sigmoideus*) (CAS, JEPS); Rademacher Hills:

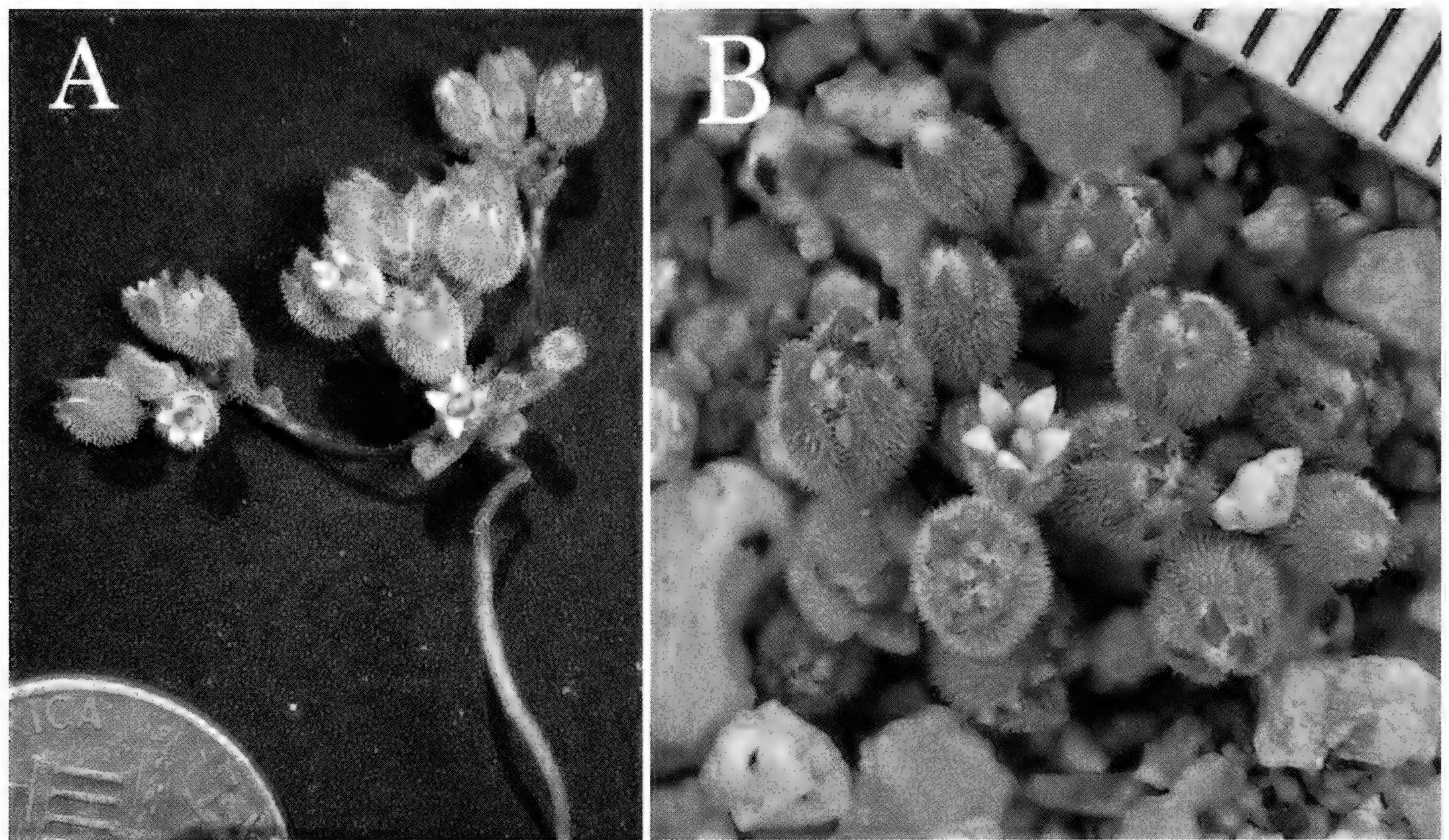


FIG. 11. *Nemacladus twisselmannii* var. *botanywomaniae* (photos K. Morse).

summit of Highway 395, Twisselmann 7063 (CAS, JEPS, SBBG); Northeast end of Buckhorn Lake, Twisselmann 10681 (CAS, JEPS, OSU, RSA, SBBG); Dunes at the northeast end of Buckhorn Lake, Twisselmann 10829 (with *N. rubescens*) (CAS, JEPS); Slope at the head of Tarweed Canyon, Twisselmann 15344 (CAS); Gravel slopes at the head of Tarweed Canyon, Twisselmann 15371 (CAS); Head of the canyon fork west of Ricardo, Twisselmann 15431 (CAS, JEPS). **Mono Co.**: south of Benton Hot Springs along Fish Slough Road, 16.1 mi north of Mono/Inyo County line, André 18403 (UCR); Benton Station, Jones s.n. (JEPS, POM). **San Bernardino Co.**: Mojave Desert; 33 air mi. NW of Barstow, c. 10 mi. north of Black Canyon, 3 mi. west of the SW corner of the Naval Weapons Center, Henrickson 17366 (RSA, UCR); Victor, Jones s.n. (US, POM); Poison Canyon, Mason 8281 (UC, US).

A New Variety of *Nemacladus twisselmannii*

Discovered in 1963 by Ernest Twisselmann, *Nemacladus twisselmannii* J.T.Howell has been known from only two localities on the Kern Plateau, totaling about 400 individuals in a 10 acre area. A new population was discovered in April 2012, in Culp Valley, Anza Borrego Desert State Park, Riverside County, a disjunction of about 350 km. The group who made the original discovery surveyed and mapped 53 plants in 2012, most in an active wash and a few in a side wash. In 2013, 23 plants were found in the original location (five in the active wash, 18 in the side wash). The type locality was considerably disturbed due to foot traffic of firefight-

ers battling the Vallecito Fire in August 2012. Similar habitats nearby were surveyed in 2012 and 2013, but no other plants were found; however, in April, 2019, about 30 plants were found in the original location. The significant geographical disjunction and presence of some notable morphological differences warrants recognition of this new population as a separate variety.

Nemacladus twisselmannii* var. *botanywomaniae Morin & T.J.Ayers, var. nov.—Type: USA. California. San Diego Co. Anza-Borrego Desert State Park, Pinyon Ridge above Culp Valley, across the road from the Wilson Trailhead; small flattish wash 2 3/4 mi SE of Ranchita, with deep sand made of small quartz grains. 33.1944–116.4844, 1214 m. Habitat: Sandy Wash in Desert Transition. *Lasthenia gracilis* (DC.) Greene, *Eriophyllum wallacei*, *Erodium cicutarium* (L.) Aiton, *Gilia diegensis* (Munz) A.D.Grant & V.E.Grant, *Stephanomeria exigua* Nutt., *Salvia columbariae* Benth., *Lotus strigosus*, *Nemacladus longiflorus* var. *breviflorus*, Apr 28, 2012. Kate Harper, Tom Chester, Keir Morse, RT Hawke, Shaun Hawke, 1712 (Holotype: SD225143!, Supplemental Figure 7).

Nemacladus twisselmannii var. *botanywomaniae* differs from var. *twisselmannii* in having the flower non-resupinate, sepals broadly deltate, and occurrence in desert habitat (Figs. 11A, B).

Stem sparsely hairy. **Leaves** often only 2 cotyledons and 2 basal leaves, which subtend the first branches, oblong-acute, 2–3.5 mm, margins entire or teeth 2, minute, surfaces hairy. **Inflorescence** bracts

ovate, 1.5–2.5 mm; pedicels 3.5 mm. **Flowers** not resupinate; hypanthium 1.6 mm, densely hairy; sepals 1.6–2.2 mm, broadly deltate, apiculate; petals connate only at base, 2 abaxial lobes divaricate, asymmetrically deltate, outer margin nearly straight, inner margin bowed, 0.5–1.5 mm, acute, 3 adaxial lobes erect, lanceolate, 0.5–1.5 mm, acute; filaments declined, connate only at apex; ovary 3/5 inferior. **Capsules** 9/10 inferior.

Distribution and ecology. Anza Borrego Desert State Park, in desert washes at 1200 m. Known only from the type locality (Fig. 10).

Phenology. Flowering June.

Etymology. The variety is named for Kate Harper, Senior Consulting Botanist and Wildlife Biologist, Harper Biological Consulting, who saw the plants first. She has been part of a group that has been documenting the plants of Anza Borrego Desert State Park for many years. When advised that the authors wished to name the plant for her in recognition of her discovery, she requested that the epithet be the name by which she is known in the group, which is Botany Woman.

KEY TO SPECIES OF *NEMACLADUS*

1. Plants prostrate or cushionlike; rosettes 1 or more, linked by leafless, prostrate branches; inflorescences capitate (sometimes somewhat elongated)
 2. Herbs 1–10 cm diam.; corolla lobes 1.5–2 mm; capsules circumscissile *Nemacladus californicus*
 - 2' Herbs 0.5–1 cm diam. or tall; corolla lobes 0.5–1.5 mm; capsules opening by valves
 3. Flowers resupinate, sepals narrowly lanceolate, Greenhorn Mountains *Nemacladus twisselmannii* var. *twisselmannii*
 - 3' Flowers non-resupinate, sepals deltate, Anza Borrego Desert *Nemacladus twisselmannii* var. *botanywomaniae*
- 1' Plants erect or spreading to decumbent; rosette 1, basal; inflorescence an open raceme
 4. Ovaries and capsules superior, capsules oblong-fusiform, urceolate, or oblong-ovoid, valves entire
 5. Corollas funnelform, pale pink or cream-colored, with wide maroon splotches *Nemacladus richardiae*
 - 5' Corollas salverform, white with maroon stripes and sometimes narrow to wide maroon blotches adaxially
 6. Corolla tube 5–8 mm; inflorescence axis often shallowly zigzag, internodes 3.5–10 mm; pedicels shallowly sigmoid *Nemacladus longiflorus*
 - 6' Corolla tube 1.5–3 mm; inflorescence axis strongly zigzag, internodes 2–5 mm; pedicels deeply sigmoid *Nemacladus breviflorus*
 - 4' Ovaries and capsules at least partially inferior, capsules round, ellipsoid, obconic, or cup-shaped, each valve splitting in two
 7. Flowers not resupinate; petals distinct nearly to base, corolla 2-lipped, lobes white or cream-colored with maroon, dark pink, or orangish or brown markings, 2 abaxial lobes declined, 3 adaxial lobes erect, filament tube declined
 8. Sepals unequal in size and shape, abaxial petals 0.4–1.6 mm
 9. Capsules round, 3–4 mm, leaves fleshy; Great Basin *Nemacladus rigidus*
 - 9' Capsules obconic, 1.5–2.7 mm, leaves not fleshy; White and Inyo mountains or Coast Ranges, Sierra Nevada, Cascade Range, and Modoc Plateau *Nemacladus morefieldii*
 10. Pedicels sigmoid; White and Inyo mountains *Nemacladus morefieldii*
 - 10' Pedicels straight or arched; Coast Ranges, w Sierra Nevada, Cascade Range, and Modoc Plateau *Nemacladus capillaris*
 - 8' Sepals equal in size and shape, abaxial petals 1.3–4 mm
 11. Basal leaf blades broadly elliptic, remaining green through flowering; corolla lobes with brown, yellow, and orange markings at tip; base of stem silver-gray *Nemacladus rubescens*
 11. Basal leaf blades oblanceolate to elliptic or ovate, generally senescing early; corolla markings maroon, base of stem brown or reddish brown
 12. Flowers with maroon or brownish maroon markings on tips of adaxial corolla lobes; deserts
 13. Capsules hemispherical, 1.5–2 mm diam.; widespread in southwestern deserts *Nemacladus orientalis*
 - 13' Capsules spherical, 3.5–4 mm diam.; central Baja California *Nemacladus australis*
 - 12' Flowers with maroon or deep pink markings near base of adaxial corolla lobes; Coast Ranges and Sierra Nevada
 14. Filaments 2 mm; capsules narrowly obconic, 2–2.5 mm; seeds 0.5 mm, with clearly pitted rows; leaf blade margins irregularly serrate; Sierra Nevada *Nemacladus interior*
 - 14' Filaments 2–2.5 mm; capsules broadly obconic, 2.5–3 mm; seeds 0.9–1 mm, with deeply impressed, vertical lines; leaf blade margins entire or obscurely toothed; Coast Ranges *Nemacladus montanus*

- 7' Flowers resupinate or not; corolla 1-lipped or nearly radially symmetric, petals usually connate 1/2–3/5 from base, lobes white or pale pink, pale blue, or pale lavender, midvein on lobes sometimes pink, lavender, or maroon, or (in *N. tenuis* var. *aliformis*) adaxial lobes orangish brown, otherwise without darker marks; filaments declined, curved, erect, or arched
15. Flowers not resupinate, corollas usually cup-shaped, white, pale pink or pale blue, sometimes with dark pink or lavender veins
16. Corollas bilaterally symmetric, 1-lipped, lobes all held on adaxial side of flower, bases of 2 lowest lobes fused into spur *Nemacladus calcaratus*
- 16' Corollas nearly radially symmetric, lobes evenly distributed, not 1-lipped, not spurred
17. Inflorescence axis straight; leaf blade margins irregularly toothed or ± pinnately lobed; bracts linear to oblong-lanceolate, erect, aligned with axis *Nemacladus ramosissimus*
- 17' Inflorescence axis zigzag or nearly straight; leaf blade margins deeply pinnately lobed; bracts linear to lanceolate or elliptic, aligned with pedicel
18. Sepals erect; hypanthium 0.5–0.7 mm; capsules hemispheric to ellipsoid; inflorescence axis nearly straight *Nemacladus pinnatifidus*
- 18' Sepals spreading; hypanthium 0.8–1 mm; capsules nearly round; inflorescence axis strongly zigzag *Nemacladus glanduliferus*
- 15' Flowers resupinate, corollas cup-shaped or tubular, white or cream-colored, sometimes lavender tinted or with tinted veins, lobes sometimes with yellow spots or tips, or adaxial lobes brownish
19. Corollas tubular
20. Corolla tube urceolate *Nemacladus sigmoideus*
- 20' Corolla tube broadly cylindric
21. Leaf blades broadly elliptic to ovate-deltate, margins shallowly toothed or wavy; inflorescence flowers not second *Nemacladus bellus*
- 21' Leaf blades narrowly lanceolate to +/– spatulate, margins deeply toothed; inflorescence flowers second *Nemacladus secundiflorus*
22. Corolla 5–6 mm, anthers 0.5–0.7 mm *Nemacladus secundiflorus* var. *secundiflorus*
- 22' Corolla 0.8–1.3 mm, anthers 0.1–0.2 mm *Nemacladus secundiflorus* var. *robbinsii*
- 19' Corollas cup-shaped.
23. Corolla lobes 2.2–3 mm
24. Anthers white or cream-colored, 0.4–0.6 mm, filament tube red to faded magenta; capsules round or broadly ovoid; sepals in fruit erect or flared from base *Nemacladus matsonii*
- 24' Anthers dark blue, 0.2–0.3 mm, filament tube dark blue to dark purple or reddish purple; capsules narrowly ellipsoid; sepals in fruit erect, flared from middle *Nemacladus parikhiae*
- 23' Corolla lobes 0.5–2.2 mm
25. Leaf blades lanceolate, oblong, or spatulate, margins deeply toothed or pinnately lobed; corollas white or cream-colored, adaxial lobes brown, deltate to nearly linear, arched, or with deep pink or pinkish brown and yellow chevrons; sepals erect in fruit, extending above capsule; filament cells cylindric, blunt
26. Corolla lobes similar, oblong-elliptic, white, tips pink or +/– yellow; capsules 1–2 mm. *Nemacladus tenuis* var. *tenuis*
- 26' Corolla lobes dissimilar, adaxial 2 linear, arched outward, maroon or brown, abaxial 3 lobes white with yellow and +/– brown markings; capsules 2–2.5 mm *Nemacladus tenuis* var. *aliformis*
- 25' Leaf blades rhombic to elliptic, narrowly oblanceolate to oblong, or spatulate, margins entire, irregularly dentate, to +/– pinnately lobed, or sharply but shallowly toothed; corollas white, cream-colored, or pale lavender, lobes unmarked or with yellow tips or with maroon line from throat to base on abaxial lobes
27. Sepals in fruit erect to spreading from base, broadly deltate, transparent cells on filaments cylindrical, obtuse; hypanthium and capsule dark purplish green, base flat, apex acute *Nemacladus inyoensis*
- 27' Sepals in fruit flared from base or clasping capsule, oblong-deltate or narrowly deltate, transparent cells on filaments attenuate, hypanthium green, capsule straw-colored, base acute, tip rounded
28. Inflorescence internodes 4–6 mm; corollas white or cream-colored with yellow markings, filaments maroon distally, anthers maroon, white or gray, 0.15–0.2 mm; capsules round; bracts narrowly lanceolate or lanceolate-ovate, 1–1.6 mm, straight or arched back *Nemacladus eastwoodiae*
- 28' Inflorescence internodes 2.5–4 mm; corollas entirely white to pale lavender, midvein on lobes lavender; filaments white, anthers white, 0.2–0.3 mm; capsules broadly obconic; bracts linear-oblong, 2–4 mm, recurved *Nemacladus gracilis*

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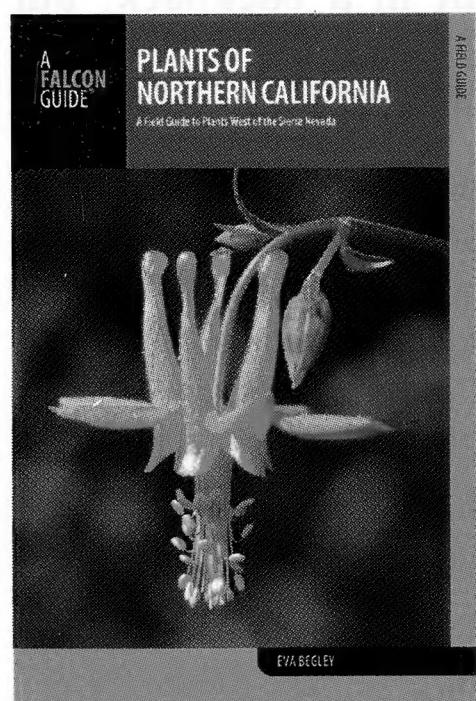
Herbarium specimens, and in some cases images of specimens, from the following herbaria were examined: ARIZ, ASC, ASU, BM, BRIT, CAS, CHICO, DS, G, GH, K, MICH, MO, NDOA, NSM, NY, OBI, ORE, OSU, PGM, POM, RSA, RENO, SBBG, SD, SDSU, TEX, UC, UCD, UCR, UCSB, UNLV, US, USU, WSU, WTU. We are grateful to these herbaria for allowing us to study their specimens, and to ASC, CAS, and JEPS/UC for receiving and housing loans. Data in the Southwestern Environmental Information Network (SEINet) and Consortium of California Herbaria have been invaluable. We thank Lois Neff for her help in the field, for providing SEM images of flowers, and for sharing her preliminary molecular phylogeny results.

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Review



Plants of Northern California, a Field Guide to Plants West of the Sierra Nevada. By EVA BEGLEY. 2018. Globe Pequot Press, Guilford, CT. 432 pages. ISBN: 1493031848, 9781493031849. Price: \$29.95, paperback edition.

Eva Begley's book, *Plants of Northern California, a Field Guide to Plants West of the Sierra Nevada*, should be hailed as a labor of love that has been long-awaited. The northern California flora is just as varied, beautiful, and scientifically interesting as the rest of the state, yet it has been historically under-explored and poorly documented. I have waited for a book like this to come out. As a young student of botany growing up in Humboldt County, I searched for texts that would help me begin to understand the plant diversity in my backyard. There are great references out there, but they are either technical (e.g., *The Jepson Manual*, Baldwin et al. 2012) or group specific (e.g., *Conifer Country*, Kaufmann 2012). *Plants of Northern California* does not cover all of the common plant species in northern California, but it makes a start. Begley's love of the flora shines in her work and hopefully will inspire other botanists to contribute to the documentation and interpretation of the northern California flora.

Begley shares her philosophy on identifying plants in the field in the introduction. She truthfully points out that many genera, such as *Arctostaphylos*, can be extremely difficult to differentiate, even for experts. She advises students of botany that it is perfectly okay to recognize these groups to genus or family, and not to let worries about species identification detract from the pleasure of observing an organism in nature — wise words indeed. This should also give the reader a sense of what to expect from the book. Begley includes common naturalized species, as well as natives, and mostly focuses on plants that are likely to be seen and understood by the casual walker. Don't expect help with the strange grass or *Ceanothus* that you can't key out. In addition, if you are looking for a book to use in the northern Sierra Nevada or the Modoc Plateau, this is not the book for you.

The introduction also covers floral morphology, including that of the Asteraceae, with a depth sufficient to allow a lay person to learn enough to

get themselves in trouble. In addition to these standard sections of botanical works, the author addresses some key questions that are often left out of field guides. These relevant questions include "What is a species?" and "Why use scientific names?" Although not necessary to enjoy the glory of a flower, these questions have the potential to deepen one's appreciation for the diversity and complexity of life. Begley also uses her discussion of scientific names to address why she organized this book by taxonomic groups rather than flower colors. I recommend that any beginning student of botany who feels daunted by this system of organization reads this section, as she lays out some excellent points.

The species treatments are organized into the Ferns and Horsetails, Conifers, Flowering plants: Dicotyledons, and Flowering plants: Monocotyledons, with the expected condition that most plants are in the Flowering plants: Dicotyledons group. Within the large groups, the species pages are organized by family, something that most experienced botanists will appreciate and that may motivate some beginning botanists to quickly learn the names and identifying features of plant families. As this book has no dichotomous keys, the end section includes a listing of plants by flower colors, which will hopefully facilitate its use by those botanists that have not yet mastered the family characteristics.

One thing that sets this guide apart from many others that I have read is the unusually intimate feeling one gets when flipping through it. The author includes details from her own experience learning these plants in a way that feels like you are out on a walk together. This passage about the smell of jimsonweed is a great example, "It reminds me of the fug on city buses in winter when I was a child in England: unwashed bodies, damp woolen clothing, cigarette smoke, the pervasive scent of soot and burning coal." Or this phrase about *Chlorogalum* flower buds, "They are said to open with an audible pop. I have watched them but never heard them. Maybe my dog did." These vivid descriptions give one the feeling of reading somebody else's field notebook, they evoke distinct events that became associated with a particular plant.

The book has other aspects of a field notebook, namely, the species included in it are reflective of the author's own experience with the flora. This means that some common or iconic plants of Northern California, at least in my mind, are not represented. Wetland plants found in the Sacramento Valley seem overrepresented. While it can be unsettling to flip through a guide and not find plants you assume to be

included, worrying over this would be missing the forest for the trees.

There are a couple of other features that should be pointed out. This book may be much more helpful to the relatively experienced botanist looking to explore outside of their area than a true novice hoping for a nice picture guide. The limitation of some of the small photos means that they might only capture an inflorescence in detail and leave out some general characters. The descriptions of other species in the same genus are helpful for botanists who are familiar with a genus, but may not add much for the beginning botanist. Finally, the large groups (Ferns, Conifers, Flowering plants) are written at the top of each page, but families are left out, which makes navigation a little difficult, as the species are organized by family. Regardless of any critiques I might have, however, I am excited to bring this book on all my future northern California excursions.

As a botanical community, we should be very glad that Eva Begley has taken the time to put this work together. It fills a much-needed niche, and should be useful to many people. We have a book to take on our walks, small enough to fit in a backpack, but versatile enough to identify many of the common plants we encounter throughout northern California.

—REED KENNY, M.S. Candidate, Department of Biology, California Polytechnic State University San Luis Obispo, 1 Grand Ave., San Luis Obispo, CA 93401.

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